PATTERNS IN SIZE, GROWTH, AND CONDITION OF JUVENILE CHUM AND PINK SALMON IN THE NORTHEASTERN BERING SEA

By

Melissa Prechtl

RECOMMENDED:

Dr. Brian Beckman

Dr. Anne Beaudreau

Dr. Megan McPhee
Advisory Committee Chair

Dr. Shannon Atkinson,
Chair, Graduate Program in Fisheries

APPROVED:

Dr. Michael Castellini
Dean, School of Fisheries and Ocean Sciences

Dr. John Eichelberger
Dean of the Graduate School

12/7/14
Date

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Melissa Prechtl, B.S.

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Abstract

The Bering Sea has alternated between warm and cool spring thermal regimes, as defined by May sea surface temperature, and in recent years has remained in a "cool" state. Differences in spring thermal regime influence the timing of sea ice extent in the southeastern Bering Sea (SEBS) region, with warm springs facilitating early ice retreats and cool springs resulting in later ice retreat. A recent conceptual model for relating production to higher trophic levels in the SEBS proposes that during years of early sea ice retreat, phytoplankton blooms occur in warm water and support small, lipid-poor species of zooplankton. Conversely, years of late sea ice retreat results in an ice associated bloom that supports large, lipid-rich species of zooplankton. As a consequence the energy density of prey sources available to higher trophic levels is reduced during warm years and enhanced during cool years. While the northeastern Bering Sea (NEBS) has consistently supported an ice-associated bloom, it is likely that productivity in the SEBS influences trophic-level connections in the NEBS. In order to examine this possibility, we extended this conceptual model to juvenile salmon and compared size and condition of juvenile chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon in the NEBS between spring thermal regimes of the SEBS. We hypothesized that juvenile salmon would be longer in warm years and more energy dense in cool years. In years with cool springs, pink salmon were shorter and chum salmon exhibited greater energy density, but no other aspects of size and condition differed significantly between spring thermal regimes. We further examined relationships of size, growth, and condition of juvenile salmon with environmental variables within the NEBS. For both species, length increased over the time of the surveys; longer individuals were caught at stations with greater bottom depths and in cooler sea-surface temperatures, while individuals with high length-corrected energy density were associated with cooler temperatures and

shallower depths. We used insulin-like growth factor-1 (IGF-1) concentrations as an indicator of relative growth rate for fishes sampled 2009-2012 and found fish exhibited higher IGF-1 l concentrations between 2010-2012 than in 2009. IGF-1 concentrations were positively correlated with temperature for juvenile chum salmon and with depth and length for juvenile pink salmon. The consistent appearance of depth (indicating distance from shore) in the best size and condition models was interpreted to indicate that as juvenile salmon moved offshore, they were allocating more energy to growth than fat storage over the course of the surveys. The association of cooler temperatures with greater energy density and longer lengths may reflect direct effects of temperature on salmon physiology as well as indirect effects on food quantity or quality indirect. Overall, recent conditions of the NEBS appear to successfully contribute to the growth and condition of the juvenile chum and pink salmon. Finally, we compared indicators of energy allocation between even and odd brood-year stocks of pink salmon and found the even brood-year stocks were more energy dense while odd brood-year stocks exhibited higher growth rates. These results reflect differences in energy allocation between brood-year stocks of juvenile pink salmon and suggest that the two brood-year stocks may respond differently to changing climate.

Table of Contents

Page

Signature Page i

Title Page iii

Abstract v

Table of Contents vii

List of Figures ix

List of Tables xi

List of Appendices xiii

Acknowledgments xv

1.1 General Introduction 1

1.1.2 Background 1

1.1.3 Physical and biological oceanography of the northeastern Bering Sea 3

1.1.4 Relationships among temperature, food availability, energy allocation, and insulin-like growth factor-1 (IGF-1) concentration in juvenile salmon 8

1.1.5 Differences in growth and condition between even and odd brood-year stocks of pink salmon 12

1.1.6 Juvenile salmon research in the sub-Arctic and this study 13

Chapter 2: Juvenile chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon growth and condition in the northeastern Bering Sea between warm and cool climate regimes 17

2.1 Introduction 17

2.2 Methods 21

2.2.1 Field sampling 21

2.2.2 Biological measurements 23

2.2.3 Statistical analysis 24

2.2.3.1 Differences in size and condition between spring thermal regimes 24

2.2.3.2 Relationships between environmental variables and size, condition, and growth 25

2.2.3.3 Model selection 28

2.2.3.4 The addition of chlorophyll-a as a predictor variable 29

2.3 Results 29

2.3.1 Variation in station location and survey timing 29

2.3.2 Differences in size and condition between spring thermal regimes 31

2.3.3 Environmental variables across stations in relation to where salmon were caught 31

2.3.4 Relationships between length and environmental variables 36
2.3.5 Relationships between weight-length residuals and environmental variables 36
2.3.6 Relationships between energy density and environmental variables 36
2.3.7 Relationships between IGF-1 concentration and environmental variables 40
2.3.8 Inclusion of Chlorophyll-a 42
2.4 Discussion 42
2.4.1 Differences in size and condition between spring thermal regimes 42
2.4.2 Relationships between physiological measures and environmental variables 46
2.5 Conclusions 50
Chapter 3: Differences in growth and condition of juvenile pink (*O. gorbuscha*) salmon between even and odd brood years within the northeastern Bering Sea 52
3.1 Introduction 52
3.2 Methods 52
3.2.1 Field sampling 54
3.2.2 Biological measurements 55
3.2.3 Statistical analysis 57
3.3 Results 58
3.4 Discussion 58
3.5 Conclusion 61
4.1 General conclusions 62
5.1 References 68

List of Figures

Page

Figure 1.1 May sea surface temperature anomalies in the southeastern Bering Sea. 7

Figure 2.1 General station locations in the northeastern Bering Sea. 22

Figure 2.2 Differences in station location and sampling time between 2003-2007 and 2009-2013 30

Figure 2.3 Juvenile chum (Red) and pink salmon (Blue) physiological measures from stations west of -166°W and east of -171°W, collected from 2003-2006 and 2009-2013.. 32

Figure 2.4 Plots from generalized additive models, using data from all years. 34

Figure 2.5 Plots of environmental variables from all stations sampled between 2003-2007 and 2009-2013... 35

Figure 2.6 Plots showing IGF-1 concentration overtime and differences between Norton Sound and Bering Sea.. 41

Figure 3.1 Differences in station location and sampling time between 2003-2007 and 2009-2013 56

Figure 3.2 Boxplots of juvenile pink salmon showing median, interquartile range, and individuals outside of interquartile range of physiological measures between odd and even brood-year stocks.. 59

List of Tables

Page

Table 2.1 Full models of juvenile salmon response against environmental predictor variables.. 26

Table 2.2 Coefficients from juvenile salmon models evaluating variation in physiological responses related to spring thermal regime..... 33

Table 2.3 Model coefficients and Akaike weights of chum salmon models with ΔAICc ≤ 2.. 37

Table 2.4 Model coefficients and Akaike weights of pink salmon models with ΔAICc ≤ 2.. 38

Table 2.5 Predictor parameter weights from models of juvenile salmon response variables against environmental variables. 39

Table 2.6 Models with chlorophyll-a were only shown in tables if the inclusion of chlorophyll-a improved model fit.. 43

Table 2.7 Predictor parameter weights from models of juvenile salmon response variables against environmental variables, including chlorophyll-a. 44

Table 3.1 Model coefficients and p-values from models testing for significant differences in juvenile pink salmon responses between even and odd brood-year stocks. 60

List of Appendices

Page

Appendix I Annual station parameter values averaged over all stations and over stations where salmon were captured. 78

Appendix II Annual station environmental parameter values averaged over all stations and over stations where salmon were captured. 79

Appendix III Number of stations surveyed each year with annual sample sizes of juvenile chum and pink salmon length, weight, calories/g, and IGF-1 concentration. 80

Appendix IV Mean annual values of juvenile salmon response variables..... 81

Appendix V Annual mean length and weight of juvenile chum and pink salmon for each response variable. 82

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1.1 General Introduction

1.1.2 Background

Changes in seasonal ice cover influence both artic and sub-Arctic regions of the North Pacific Ocean. Sea ice extent and timing of sea ice retreat in the Bering Sea influences climate and ecosystem function of the region (Overland and Stabeno 2004). In the northeastern Bering Sea (NEBS), consistent seasonal ice coverage and timing of sea ice retreat results in tight pelagic-benthic coupling (Grebmeier et al. 2006a). Cool water temperatures limit zooplankton grazing and consequently, production sinks to the benthos supporting a rich and diverse benthic community (Dunton et al. 2005; Grebmeier et al. 2006a). The extent and timing of sea ice retreat is variable in the southeastern Bering Sea (SEBS), alternating between years of early and late sea ice retreat (Hunt et al. 2011). Warmer water temperatures during years of early ice retreat in the SEBS facilitate a decrease in pelagic-benthic coupling, with more production remaining in the pelagic system (Overland and Stabeno 2004; Hunt et al. 2011). Increased pelagic production in both Arctic and sub-Arctic regions has coincided with recent northward expansion of many marine organisms, including salmon (Bendock 1979; McElderry and Craig 1981; Craig and Haldorson 1986; Babaluk et al. 2000; Overland and Stabeno 2004; Grebmeier et al. 2006a; Moss et al. 2009). In addition, increases in production parallel reported increases in the abundance of salmon by subsistence users in northwestern Alaska (Eggers et al. 2011; Carothers et al. 2013) and have raised interest in the implications of reduced seasonal sea ice on salmon harvest in the future. These concerns are reflected by policy that addresses balancing the ecological, social, and economical aspects of management in a rapidly changing environment (U.S. ARC 2012).

Despite recent increases in salmon production reported by subsistence users at the northern edge of the range of salmon in Alaska, declines in western Alaska's salmon stocks in the late 1990s and early 2000s resulted in an economic disaster for people whose livelihoods depend on salmon resources (Myers et al. 2006). This hardship was recognized at the federal level in 1997, when the U.S. Department of Commerce used its legislative authority, under section 312(a) of the Magnuson-Stevens Act, to declare a commercial fishery failure (Myers et al. 2006). In response, the U.S. government, and other North Pacific Anadromous Fish Commission nations, implemented the Bering Aleutian International Survey (BASIS) in 2002 (Myers et al. 2006). The major goal of BASIS was to elucidate the mechanisms linking ocean condition to salmon abundance in the Bering Sea.

Cold-water tolerance and short residence time in freshwater allow chum and pink salmon to colonize novel habitat and make them likely candidates for future northern range expansion (Craig and Haldorson 1986; Irvine et al. 2009; Nielsen et al. 2012). However, there is a lack of scientific studies that investigate the use of high latitude habitats by salmon. With local residents in northern Alaska testifying that more salmon are being caught in their subsistence fisheries (Eggers et al. 2011; Carothers et al. 2013) and the possibility of salmon populations expanding northward as climate continues to warm, it is imperative that research assesses the northeastern Bering Sea (NEBS) as productive salmon habitat. Because of their commercial and subsistence importance and cold-water tolerance, juvenile chum and pink salmon should be the focus of future research.

In this introductory chapter, I briefly synthesize the oceanography of the NEBS to provide an overview of the environmental conditions that juvenile salmon in the NEBS experience. This will be followed by a brief literature review on the relationships among

temperature, diet, energy allocation, and insulin-like growth factor-1 (IGF-1) concentration of juvenile salmon. A short section will focus on hypothesized differences in energy allocation between even and odd stocks of pink salmon. Finally, a summary of recent scientific observations of juvenile salmon in the sub-Arctic and Arctic regions will provide the basis for the thesis chapter describing juvenile chum and pink salmon growth and condition in warm and cool climate regimes of the NEBS.

1.1.3 Physical and biological oceanography of the northeastern Bering Sea

Three ocean currents contribute to the productivity of the Bering Sea (Weingartner 1997; Norcross et al. 2010). The Anadyr Water (AW) transits north on the western side of the Bering Sea, the Alaska Coastal Water (ACW) flows north on the eastern side of the Bering Sea, and the Bering Shelf Water (BSW) runs northward in-between the AW and ACW. Compared to the ACW, the AW is characterized as having cooler sea surface temperatures (SST), higher sea surface salinities (SSS), and being nutrient rich. Compared to the BSW and AW, the ACW is characterized as having warmer SSTs, lower SSSs, being nutrient poor, and dominated by small zooplankton taxa (Eisner et al. 2012). Compared to the ACW, the BSW is characterized as having cooler SSTs, higher SSSs, higher chlorophyll and nutrient levels, and supports populations of large zooplankton taxa (Eisner et al. 2012). Within the NEBS, the distribution of these currents creates temperature and salinity gradients, with SST and SSS increasing with distance from shore. The gradual increase in bottom depth with distance from shore within the NEBS also contributes to the SST gradient. However, annual variability in weather, wind, and seasonal sea ice patterns drives variability in the distribution of currents.

As seasonal sea-ice melts, these water masses mix as they move northward, providing nutrient rich water to the Chukchi Sea (Grebmeier et al. 2006b). High concentrations of nutrients and long summer photoperiod result in the high primary productivity observed in the sub-Arctic and Arctic. However, low water temperature limits grazing pressure on primary production, resulting in high export of carbon to the sea floor (Springer et al. 1996; Coyle and Pinchuk 2002). This influx of carbon provides a major food source for benthic organisms and results in the benthic-dominated system that is characteristic of the sub-Arctic and Arctic regions. Yet, warming temperatures and declines in seasonal sea ice are resulting in increases in primary production (Pabi et al. 2008; Brown and Arrigo 2013). More energy is being taken up by the pelagic food web as temperature limitation on zooplankton grazing is reduced, initiating a shift from a benthic to pelagic-dominated system (Hunt and Stabeno 2002; Grebmeier 2006b; Marinov et al. 2010).

The northward flow of ocean currents results in many similarities in ecosystem community structure between the northeastern Bering Sea and the southern Chukchi Sea. Sigler et al. (2011) found zooplankton taxa within the NEBS were more similar to those within the Chukchi Sea than those in the southern Bering Sea. Furthermore, results from Matsuno et al. (2011) showed an increase in influx of warm, nutrient rich Pacific water from the Bering Sea into the Chukchi Sea from 1991 to 2007. As a consequence, the zooplankton community structure within the Chukchi Sea was composed of a higher proportion of Pacific copepod species in 2007, compared to 1991. Expanded distribution of Pacific zooplankton species may facilitate the expansion of other pelagic species, such as juvenile salmon into the Chukchi Sea. These results highlight the similarity in ecosystem function between the NEBS and the Chukchi Sea and suggest that the Chukchi Sea may provide suitable habitat for juvenile salmon. However,

baseline knowledge of how ocean conditions within the NEBS are related to growth and condition of juvenile salmon is needed in order to monitor increases and/or northward expansion into Arctic habitat.

The extent and timing of sea ice retreat are the dominant factors controlling ecosystem function in the Bering Sea (Hunt and Stabeno 2002; Stabeno et al. 2010; Hunt et al. 2011). It is the melting of the sea ice that initiates the spring phytoplankton blooms. Hunt et al. (2011) put forth the Oscillating Control Hypothesis (OCH) as a mechanism for describing how the timing of sea ice retreat affects the spring phytoplankton bloom, copepod production, and walleye pollock (*Gadus chalcogrammus*) recruitment in the SEBS. The OCH proposes that in years of early ice retreat, the spring phytoplankton blooms occurs in warm, open-water that facilitates the production of small species of copepods. Conversely, during years of late ice retreat, the spring phytoplankton bloom occurs at the ice-edge in cold water and facilitates the production of large species of copepods. These large species of copepods are lipid-rich, providing an energy dense food source for juvenile walleye pollock and thus increasing their over-winter survival (Heintz and Vollenweider 2010). This hypothesis may provide a mechanism linking primary and secondary production to other planktivorous species, such as juvenile salmon. However, the applicability of this hypothesis to other consumer taxa, as well as at higher latitudes, has yet to be rigorously tested (Brown and Arrigo 2013). Furthermore, the inter-annual variability in oceanography and atmospheric forcing add to the complexity of the physical and chemical dynamics influencing ecosystem structure within the sub-Arctic and Arctic regions of the Bering Sea.

While we have cited similarities in oceanography between the NEBS and the Chukchi Sea (Sigler et al. 2011; Eisner et al. 2012), it is important to recognize that there are clear

differences in weather and climate patterns north and south of the Bering Strait. For example, as seasonal sea-ice extent and duration continues to decrease in the Arctic, the Bering Sea ice cover reached a 30-year high in the winter of 2007-2008 (Sigler et al. 2011). Factors such as bathymetry, currents, and latitude all play influential roles in determining how ocean condition will be affected by increased climate variability, and how different regions of the Arctic will respond to changes in climate differently (Sigler et al. 2011).

In recent years, the SEBS has alternated between warm and cool spring thermal regimes. Years 2002 to 2005 were characterized by anomalously warm May spring sea surface temperatures and early sea ice retreats and since 2006, the region has been characterized by anomalously cool May spring sea surface temperatures and late sea ice retreats (Figure 1.1; Andrews et al. 2009; Farley and Trudel 2009; Overland et al. 2012). Warm years were found to support open-water spring blooms that experienced a 70% increase in primary production (Brown and Arrigo 2013). In the SEBS, these open water blooms supported warm-water species of zooplankton that were lipid-poor, reducing the amount of energy available to higher trophic levels (Hunt et al. 2011). Conversely, ice-associated blooms that occurred during years of late ice-retreat supported lipid-rich, cold-water species of zooplankton, increasing the amount of energy available to higher trophic levels (Hunt et al. 2011). Thus, it has been interpreted that ice-associated blooms provide an energy dense prey source for juveniles of walleye pollock and other pelagic species, such as salmon.

In contrast, the NEBS does not experience inter-annual variability in sea ice retreat and instead is always characterized by a cold, ice-associated bloom (Brown and Arrigo 2013).

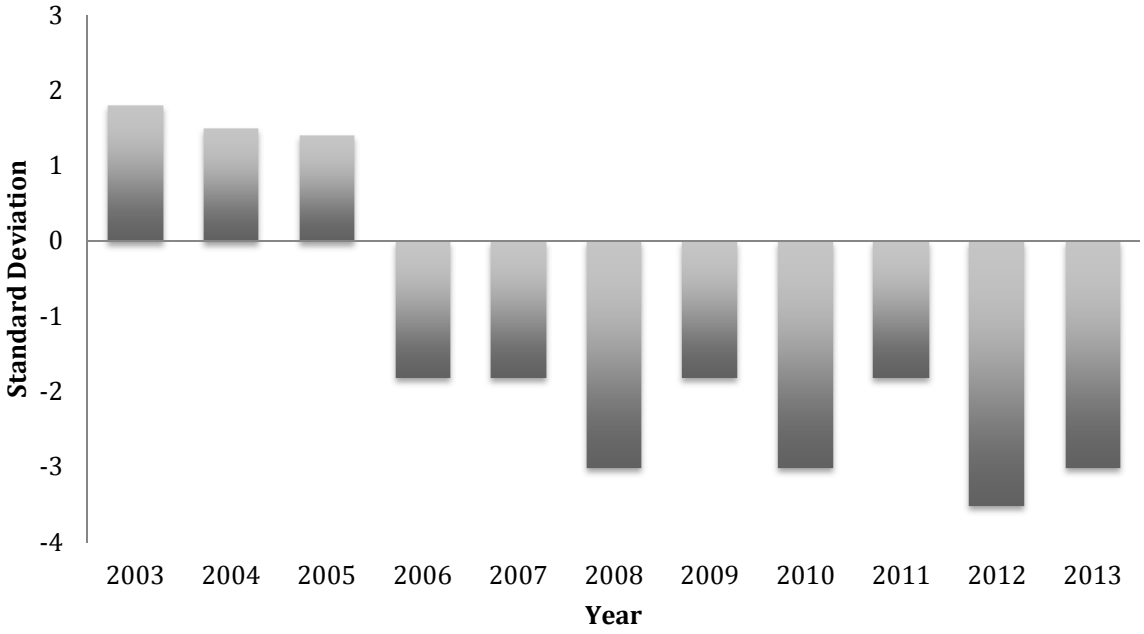


Figure 1.1 May sea surface temperature anomalies in the southeastern Bering Sea. Plot based off of figure from www.beringclimate.noaa.gov.

However, Brown and Arrigo (2013) did observe differences in primary production in the NEBS coinciding with the warm and cool spring thermal regimes of the SEBS. During years of early ice retreat in the SEBS, the authors observed that spring blooms in the NEBS were twice as productive (Brown and Arrigo 2013).

The warm years experienced in the SEBS might provide a snapshot of predicted future conditions within the Bering Sea. However, as temperatures continue to warm, there exists considerable uncertainty regarding how changes in ice cover will influence ecosystem dynamics. Comparing the effect of warm and cool spring thermal regimes of the SEBS on the NEBS can provide insight on how the NEBS may function in the future. Furthermore, understanding connection among environmental parameters and juvenile salmon characteristics in the NEBS will help us to understand how current ecosystem processes in the NEBS support juvenile salmon.

1.1.4 Relationships among temperature, food availability, energy allocation, and insulin-like growth factor-1 (IGF-1) concentration in juvenile salmon

It has been hypothesized that marine survival of salmon is dependent on early marine growth, particularly growth accrued over the first summer in the ocean (Beamish and Mahnken 2001; Farley et al. 2007). Growth is dependent on several factors, including water temperature, quality and quantity of prey sources, and photoperiod (Beckman et al. 2004a). Growth is also dependent on a predator's ability to access prey, which can also be affected by environmental factors that influence foraging, such as temperature and photoperiod. Warmer temperatures increase metabolic rates (Clarke and Johnston 1999). If dietary needs are met and water temperatures do not exceed thermal limits, increases in temperature usually result in longer, faster growing fish. Conversely, cooler temperatures will decrease metabolism, resulting in

reduced ability to capture and digest prey items. However, studies have shown the direct and indirect effects of cooler temperature positively affecting organisms inhabiting marine environments. For example, lipid-rich species of copepods are associated with cooler temperatures and currents, providing an energy dense prey source for higher trophic levels (Hunt and Stabeno 2002; Coyle et al. 2011; Hunt et al. 2011; Mueter et al. 2011). Cooler sea surface temperatures are also associated with wind-mixing events and eddy induced upwelling, both of which increase nutrient levels in surface waters and serve to increase productivity (Spall 2007; Mueter et al. 2011). Additionally, studies have shown cooler temperatures have also been found to have physiological effects on energy allocation for salmonid species. Studies have shown that cooler water temperatures result in an increase of whole body energy content (WBEC) in coho (*O. kisutch)* and pink salmon, regardless of diet (Andrews et al. 2009; Heintz 2009). Salmonids with a higher WBEC have increased their odds of surviving periods of reduced food availability, such as winter. Salmonids allocate energy to length and fat storage, thus an energy dense diet may result in increases in lipid content, increases in length, or both.

Andrews et al. (2009) investigated the influence of warm and cool spring thermal regimes on the diet and growth of juvenile pink salmon in the eastern Bering Sea. They found that juvenile pink salmon in the eastern Bering Sea fed on higher quality prey sources during warm years and were significantly longer compared to juveniles caught in cool years. However, juvenile pink salmon caught in cool years had higher WBEC. Lab studies have yielded similar results. Heintz (2009) found that when juvenile coho salmon were raised in two temperature treatments and fed *ad libitum,* fish in cooler temperatures had higher WBEC. These results suggest that salmonids allocate more energy to storage in cooler water temperatures. Cooler

temperatures may serve as a physiological signal for juvenile salmon to switch from allocating energy to length to allocating energy to storage in preparation for winter.

The idea that prey quality versus quantity is more important to survival is challenged by results from a study by Armstrong et al. (2008). The study sampled juvenile pink salmon in Prince William Sound and the Gulf of Alaska, and found a positive correlation between pink salmon growth and survival and a diet dominated by pteropods and high stomach fullness. Pteropods are low-lipid content prey source, suggesting that in some cases, quantity might be more important than prey quality (Davis et al. 1998). However, these results may simply reflect the ability of juvenile pink salmon to exploit lower trophic levels giving them a competitive advantage over other salmon species and resulting in increased survival (Kaeriyama et al. 2000; Ruggerone and Nielson 2004). Additionally, the effects of prey quality and quantity on salmon condition are likely to vary from year to year and region to region.

The endocrine system regulates physiological processes such as growth and is influenced by a fish's thermal and nutritional environment. Therefore, growth hormones, such as insulin-like growth factor-1 (IGF-I), have been proposed as possible indicators of somatic growth (Beckman 2011). Growth hormone (GH) stimulates hepatic production of IGF-I in fishes (Cao et al. 1989; Duan et al. 1993; Duguay et al. 1994). IGF-I stimulates muscle and cartilage growth and previous studies have shown IGF-I concentration to be an accurate measure of relative growth rate in many teleost species (Funkenstein et al. 1989; McCormick et al. 1992; Negatu and Meier 1995; Chen et al. 2000). The ability of the liver to utilize GH is controlled by overall nutritional status (Beckman 2011). Multiple studies have concluded that a positive relationship exists between feeding level, IGF-I concentration, and growth (Duan et al. 1993; Perez-Sanchez et al. 1995; Beckman et al. 1998; Larsen et al. 2001; Mingarro et al. 2002).

Studies of juvenile coho salmon and gilthead sea bream (*Sparus aurata*) have shown concordance between growth and IGF-I concentrations regardless of diet composition (Perez-Sanchez et al. 1995; Beckman et al. 2004b,c; Beckman 2011). A review of the literature suggests that the relationship between feeding level and IGF-I concentration is strongest when integrating growth over a 2-4 week period, providing further evidence of IGF-I concentration as a measure of recent relative growth and feeding level (Beckman 2011). For example, if fish sampled from a specific area are able to maintain a feeding level that promotes growth, then their IGF-1 concentrations will be higher than that of a fish sampled from an area with reduced prey availability. As such, in addition to providing information on relative growth rate of juvenile salmon, IGF-1 concentration may also be useful to infer feeding success in a region. For example, IGF-I concentration was positively correlated with the proportion of non-empty stomachs in lingcod (*Ophiodon elongatus)* sampled in the San Juan Islands, WA (Beaudreau et al. 2011). However, while there is concordance between IGF-1 concentration and feeding level, this relationship has yet to be fully investigated at differing temperatures (Beckman 2011). Since metabolic pathways of poikilotherms are correlated with temperature, it is possible that low temperatures may result in discordance between IGF-1 concentration and feeding level. While at lower temperatures, feeding, growth, and IGF-1 concentration are all reduced, the relationships among growth, IGF-1 concentration, and feeding level at lower temperatures have yet to be investigated.

In recent years, catches of salmon throughout Alaska's sub-Arctic have increased, with 80% of catches comprised of chum and pink salmon (Beamish 2012). Historically high catches occurred in 2007 and 2009 (Beamish 2012). These years are categorized as being "cool" years, based on May spring sea surface temperature anomalies within the SEBS (Andrews et al. 2009;

Farley and Trudel 2009; Overland et al. 2012). As discussed in the previous section, cooler temperatures in the SEBS influence the energy available to higher trophic levels. In addition, recent studies have shown an increase in the advection of large lipid-rich Pacific zooplankton taxa into Arctic regions (Matsuno et al. 2011; Sigler et al. 2011). Thus, the current cool climatic regime of the Bering Sea may be having a positive effect on the growth and condition of salmon inhabiting the northern waters of the Bering Sea. If feeding conditions for juvenile salmon are improving in the NEBS, this could result in increased use of sub-Arctic and even Arctic habitat as summer feeding grounds for juvenile salmon, supporting growth, and encouraging northward movement. However, it is important to keep in mind that the low winter sea surface temperatures of the Chukchi and NEBS regions can be lethal for salmon. Irvine et al. (2009) outlined three hypotheses to explain how salmon survive Arctic winter temperatures, all of which involve salmon migrating out of surface Arctic waters.

1.1.5 Differences in growth and condition between even and odd brood-year stocks of pink salmon

Pink salmon (*Oncorhynchus gorbuscha*) have a unique two-year life cycle, with even and odd stocks (with 'even' and 'odd' referring to brood year) being genetically distinct (Apsinwall 1974; Beacham and Murray 1988; Beacham et al. 2012). Consistent with their short life cycle, juvenile pink salmon have the highest early marine growth rates of Pacific salmon (Ricker 1976; Brett 1979). Beamish (2012) suggested that strong genetic differences between even and odd pink salmon stocks might also include differences in energy allocation, with even stocks allocating more energy to storage, and the odd stocks allocating more to growth, during the summer growing season. Data used in this thesis provide the opportunity to test for differences in energy allocation between even and odd stocks of juvenile pink salmon inhabiting the NEBS.

1.1.6 Juvenile salmon research in the sub-Arctic and this study

In response to declines in western Alaskan salmon stocks in the late 1990s, the U.S. government, and other North Pacific Anadromous Fish Commission nations, implemented the Bering Aleutian International Survey (BASIS) in 2002 (Myers et al. 2006). The major goal of the annual BASIS surveys was to elucidate the mechanisms linking ocean condition to salmon abundance in the Bering Sea. The early years of BASIS corresponded with the recent warming event in the Bering Sea from 2002 to 2005, and BASIS extended into the cool years, 2006 to 2011. Despite recent cooling in the Bering Sea, it has been proposed that changes in climate may result in increased productivity in the Bering Sea and other high latitude regions (Grebmeier et al. 2006a; Brown and Arrigo 2013). The BASIS surveys included physical and biological oceanographic sampling and may be used to monitor possible changes in pelagic productivity in high latitude regions within the Bering Sea.

The BASIS surveys provide a sufficient range of variation in spring thermal conditions to allow researchers to examine thermal regime effects on salmon production within the Bering Sea. A review of BASIS salmon food habits study by Davis et al. (2009) compared zooplankton composition and juvenile salmon diet between the western and eastern Bering Seas. In the eastern Bering Sea, authors reported an increase in abundance between 2006-2008 in the large zooplankton (Davis et al. 2009). Concurrent with the increase in large zooplankton abundance, Volkov et al. (2007) found increases in the proportion of large zooplankton in salmon diets. While larger zooplankton dominated during cool years, smaller-sized zooplankton were predominant in warm years (Davis et al. 2009). These results reflect changes in zooplankton composition and salmon diet within the NEBS between spring thermal regimes of the SEBS, suggesting that spring thermal regime may influence ecosystem dynamics within the NEBS.

Farley and Moss (2009) examined growth rate and abundance of juvenile chum salmon (*O. keta*) in the NEBS and the SEBS between warm (2002-2005) and cool (2006-2008) years. The authors found that in the NEBS, juvenile chum salmon were more abundant and experienced increases in growth rate during cool years. However, juvenile chum salmon were significantly longer in the NEBS during warm years (Farley and Moss 2009). Sampling took place between August and September, during the latter part of the first summer at sea for juvenile salmon. The authors suggested their results of smaller, faster growing fish observed during the cool years reflect that smaller juvenile chum salmon allocate more energy to growth towards the end of their first summer at sea (Farley and Moss 2009). These results could also be explained by the cumulative effect of temperature in the ocean. During cooler years, temperatures may not promote growth of juvenile salmon until the latter part of their first summer at sea. At this time, the effects of temperature and prey availability may result in the enhanced growth rates observed in juvenile salmon during cool years.

While the BASIS surveys have provided insight on the food habits and distribution of juvenile salmon inhabiting the Bering Sea, little attention has been focused on how ocean conditions of the NEBS support juvenile salmon growth and condition. This is likely due to the greater densities of salmon being surveyed in the SEBS. However, in 2007, BASIS surveys expanded into the NEBS and Chukchi Sea and found greater abundances of juvenile chum and pink salmon in the Bering Strait region and the Chukchi Sea compared to the rest of the NEBS (Moss et al. 2009). Furthermore, Moss et al. (2009) found that juvenile chum and pink salmon in the Bering Strait region and Chukchi Sea regions had faster growth rates and fed on higher energy prey than those sampled south of the Bering Strait region. These findings suggest that prey availability and habitat conditions in these sub-Arctic and Arctic regions are conducive to

survival and growth of juvenile salmon. However, it remains unclear as to whether or not these regions consistently provide the resources necessary to promote the survival of juvenile salmon. Furthermore, we lack baseline knowledge of relationships between environmental variables and juvenile salmon growth and condition in the Arctic region.

This thesis will provide information on how spring thermal regimes in the SEBS influence juvenile chum and pink salmon size and body condition inhabiting the NEBS. In addition, we will examine relationships within the NEBS between juvenile salmon size, growth, and condition and environmental variables. This study will use length (mm) as an indicator of somatic growth, weight-length residuals and energy density (calories/g) as indicators of salmon body condition, and insulin-like growth factor-1 (IGF-1) concentrations as an indicator of relative growth rate. These responses are directly influenced by physical and biological oceanographic factors and therefore can be used to make inferences about the conditions in the NEBS conducive to the growth and condition of juvenile salmon.

Data collected from the BASIS surveys (2003-2007; 2009-2011) will be combined with the two consecutive years of sampling by the Arctic Ecosystem Integrated Survey (Arctic Eis) project (2012 and 2013) to investigate how environmental variability of the NEBS affect juvenile salmon size, growth, and body condition. Results from this study will provide a baseline of juvenile salmon growth and condition within the NEBS. Similarities between the NEBS and Chukchi Sea suggest that results from this study can be applied to future studies investigating juvenile salmon in the Arctic. This study will increase current understanding of the relationships between spring thermal regimes, size, growth, and body condition of juvenile salmon. This information on early marine growth and body condition of juvenile salmon in the NEBS region

will benefit salmon fisheries in the State of Alaska and will be useful for adaptive management strategies as the sub-Arctic and Arctic climate continues to warm.

Chapter 2: Juvenile chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon growth and condition in the northeastern Bering Sea between warm and cool climate regimes

2.1 Introduction

Chum and pink salmon provide vital ecological, economic, and subsistence resources to the peoples of western Alaska. Chum and pink salmon are broadly distributed across the Pacific Ocean and inhabit the most northern range extent of Pacific salmon, with a few populations natal to Alaska's North Slope rivers (Irvine et al. 2009). The cold water tolerance of these species and their minimal use of freshwater habitat have enabled populations to colonize sub-Arctic and Arctic regions (Craig and Haldorson 1986; Irvine et al. 2009). These characteristics make chum and pink salmon likely candidates for future northern range expansion as Arctic climate continues to warm (Nielsen et al. 2012). In recent years, populations of chum and pink salmon in the North Pacific Ocean have increased due primarily to increased hatchery production but also enhanced marine survival (Ruggerone et al. 2010). Furthermore, significant abundances of juvenile chum and pink salmon have been observed in the NEBS and southern Chukchi Sea (Moss et al. 2009). These observations parallel reported increases in the abundance of salmon by subsistence users in Arctic and sub-Arctic habitats in northwestern Alaska (Eggers et al. 2011).

Previous studies have shown the NEBS to be important summer feeding habitat for juvenile salmon of Western Alaska (Andrews et al. 2009; Cieciel et al. 2009; Farley et al. 2009; Moss et al. 2009; Sigler et al. 2011). Recent climatic trends and changes in large-scale ocean processes, such as fluxes in the Aleutian Low and changes in seasonal sea ice extent, have bottom-up ecosystem effects and are believed to be responsible for fluctuations in abundances of salmon populations (Grebmeier et al. 2006a; Moss et al. 2009; Agler et al. 2013; Murphy et al. 2013). Climate variability in the Bering Sea and warming in the Arctic will continue to

complicate efforts to forecast and manage salmon returns. Therefore, it is important to investigate how changes in climate correspond to condition and growth of juvenile salmon.

In the 2000s, conditions in the SEBS region transitioned from a warm to cool spring thermal regime, as defined by anomalies in May sea surface temperatures (SST). This transition was unusual in the context of the past 95 years of climate history in the Bering Sea (Overland et al. 2012). From 2002 to 2005, the region experienced anomalously warm May SSTs and early spring ice retreats. Since 2006, the region has experienced anomalously cool May SSTs and later spring ice retreats (Davis et al. 2009; Stabeno et al. 2012a; see Chapter 1, Figure 1.1). Climate variability in the Bering Sea has had profound effects on ecosystem dynamics, which are largely dictated by the timing and extent of seasonal sea ice (Hunt and Stabeno 2002; Grebmeier et al. 2006a; Cieciel et al. 2009; Farley et al. 2009; Hunt et al. 2011; Sigler et al. 2011; Stabeno et al. 2012a). It is the timing of sea ice retreat that characterizes the spring phytoplankton bloom and determines productivity levels that shape ecosystem dynamics the following summer (Farley et al. 2009; Brown et al. 2011; Hunt et al. 2011). In addition to setting the stage for summer productivity in the Bering Sea, spring ice break-up determines the timing of juvenile salmon movements in western Alaska, with salmon generally distributed in warmer SSTs (Straty 1974; Farley et al. 2005). While our understanding of spring thermal regimes on ecosystem dynamics in the SEBS has increased, there is limited knowledge regarding how changes in productivity levels in the SEBS influence dynamics in the NEBS. Additionally, our understanding of how ocean conditions within the NEBS are related to the growth and body condition of juvenile salmon is limited.

It has been hypothesized that marine survival of salmon is dependent on early marine growth particularly growth accrued over the first marine summer (Beamish and Mahnken 2001;

Farley et al. 2007). It has been proposed that marine survival is also dependent on juvenile salmon reaching threshold levels of nutritional condition (from hereafter referred to as 'condition'), in order to survive their first marine winter (Beamish and Mahnken 2001). There is a strong correlation between growth and temperature, given that nutritional needs are met and temperatures are within the thermal limits of the organism (Larson et al. 2001; Beckman et al. 2004c; Andrews at al. 2009). However, temperature has been shown to have contrasting effects on growth and condition of juvenile salmon (Andrews et al. 2009; Davis et al. 2009; Heintz 2009). Andrews et al. (2009) found that juvenile pink salmon in the NEBS were longer but less energy dense during warm years. Lab studies have also shown cooler temperatures facilitate lipid storage in juvenile salmon (Heintz 2009). Continued investigations of how the SBS spring thermal regime affects growth and condition of juvenile chum and pink salmon in the NEBS will increase our understanding of how salmon might respond to future changes in climate.

Fish body condition can be evaluated using different measures of condition. Multiple condition indices complement each other to provide a more holistic view of juvenile salmon physiology. The necessity of assessing multiple responses is evident by previous studies showing no strong relationships between body size and energy density (Trudel et al. 2005; Rodgveller et al. 2007). Body condition is an indicator of nutritional state (Jakob et al. 1996). Weight-length residuals provide a simple method for assessing body condition while controlling for variation in body size (Jakob et al. 1996). While weight-length residuals allow us to compare condition between individuals, they do not provide us with any information on body composition. Energy density, measured as calories/g in our study, provides a measure of protein and lipid content and is therefore an indicator of how much energy a fish has stored. While the literature emphasizes the importance of length for marine survival of juvenile fish, it is hypothesized that energy

density plays a pivotal role in overwinter survival, when prey resources are reduced (Beamish and Mahnken 2001).

In this study, we used length as an indicator of size, and Insulin-like growth factor-1 (IGF-1) concentration as an indicator of recent growth rate. Length serves as an indicator of the amount of energy dedicated towards somatic growth. Insulin-like growth factor-1 (IGF-1) concentration was measured as an indicator of recent growth rate. As part of the endocrine system, regulating growth hormones such as IGF-1, have been proposed as possible indicators of somatic growth (Beckman 2011). A review of the literature suggests that the relationship between feeding level and IGF-1 concentration is strongest when integrating growth over a 2-4 week period, providing further evidence of IGF-1 concentration as a measure of recent relative growth and feeding level (Beckman 2011).

We used data from the Bering Sea from 2003 to 2013 to examine how spring thermal regime and summer ocean conditions influence size, growth, and condition of juvenile salmon in the NEBS. Specifically, our objectives were to 1) determine whether size (length) and condition significantly differed between warm and cool spring thermal regimes, and 2) determine how size, condition, and growth were related to environmental variables using generalized linear models. Our results provide a foundation for understanding how climate-induced changes in habitat may affect condition and growth of juvenile salmon. We hypothesized that salmon would be shorter but in better condition during the cool spring thermal regime based on expected trophic consequences of ice-associated bloom in the SEBS.

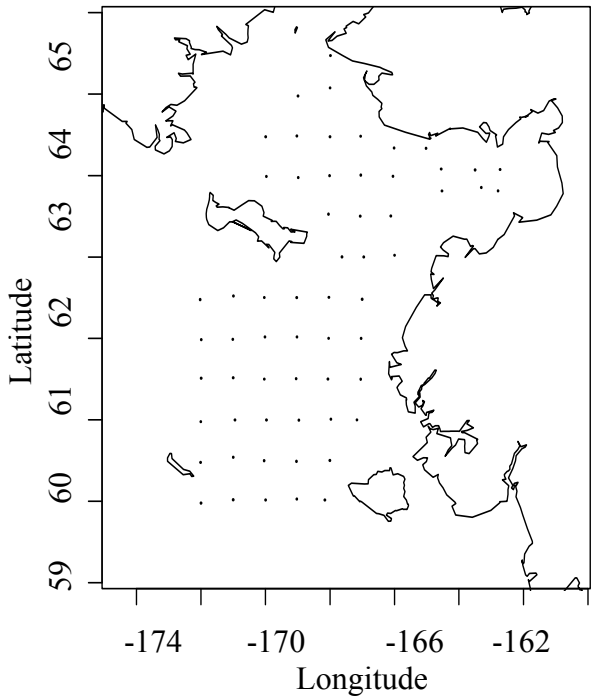
2.2 Methods

2.2.1 Field sampling

Surveys were conducted each September from 2003 to 2013 (except 2008) in the Bering Sea. Over the course of the surveys, there were variations in station latitude, longitude, depth, and Julian day of sampling (Figure 2.1; Appendix I). In addition, there was also annual variation in environmental parameters (Appendix II) and the number of stations sampled where chum and pink salmon were captured (Appendix III). Juvenile salmon were collected using a midwater rope trawl (model 400/300) made by Cantrawl Pacific Limited of Richmond, B.C., Canada. The net was approximately 198 m long and had hexagonal mesh in the wings and body, a 1.2-cm mesh liner in the cod-end, and a mouth opening of approximately 55 m horizontally by 15 m vertically. It was towed at or near the surface for 30 minutes at speeds between 3.5 and 5 knots at each station. More detailed descriptions of surface trawl operations are given in Murphy et al. (2003) and Farley et al. (2009). All sampling was done during daylight hours, from approximately 0700 AKDT to 2300 AKDT. Standard biological measurements, including fork length and body weight, were recorded.

Oceanographic data were collected at each trawl station immediately prior to deploying the trawl. Vertical profiles of temperature, salinity, chlorophyll-a fluorescence, light transmission, and photosynthetic available radiation (PAR) were measured with a Sea-Bird Electronics Inc. SBE 25 Sealogger Conductivity-Temperature-Depth profiler (CTD). Surface temperature and salinity data were measured continuously with a thermosalinograph mounted aboard the ship. During 2013, flooding aboard the vessel resulted in the loss of juvenile pink and chum salmon whole-body and blood samples.

(a)



(b)

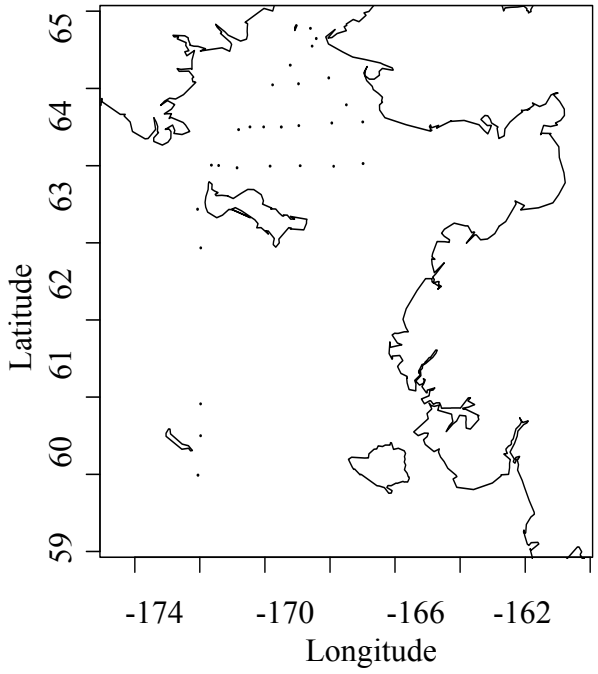


Figure 2.1 General station locations in the northeastern Bering Sea. (a) 2003-2006; 2009-2013 and (b) 2007.

2.2.2 Biological measurements

Length was used to assess size of juvenile chum and pink salmon. Condition was assessed by weight-length residuals and length-specific energy density (calories/g). The fork length (to the nearest mm) and weight (to the nearest gram) of up to 50 haphazardly sampled fish of each species sampled at each station (Appendix IV; Appendix V). A linear regression of natural log-transformed weight (g) against natural log-transformed length (mm) was performed. Regressions were calculated for each species separately, pooled over stations and years. Length-weight residuals were calculated from the fitted models and used as an index of body condition (Farley et al. 2005).

Two individuals per species and station were haphazardly sampled for whole-body samples to assess energy density (Appendix IV; Appendix V). Whole bodies of juvenile salmon were stored at -80°C and shipped to Ted Stevens Marine Research Institute (TSMRI) in Juneau, AK, at the end of the cruise. At TSMRI, juvenile chum and pink salmon energy densities were determined using bomb calorimetry, following the method described by Andrews et al. (2009). Prior to bomb calorimetry, fish were weighed (g) and otoliths and stomach contents were removed. Fish were dried in a VWR 1324 convection oven at 60-65° C until a constant weight (within 0.005 g) was obtained. Individual fish were then homogenized using a pulverizer for 30 seconds and then transferred to a mortar and pestle and pulverized further until a uniform powder was obtained. For each sample, pellets were pressed using approximately 0.15 g of powder. Pellets were then combusted in a Parr 1425 Semimicro calorimeter to determine whole-body energy content (WBEC). The values generated by the calorimeter were then converted from calories/g dry weight to calories/g wet weight.

IGF-1 was used as an indicator of relative growth rate. IGF-1 concentrations were determined via blood samples from up to 10 individuals of each species from each station (Appendix IV; Appendix V). Fish were bled using a heparinized syringe to draw blood from the ventral side of the caudal peduncle. Bleeding of fish < 130mm in length was accomplished by cutting the tail off at an angle at the caudal peduncle and collecting the blood in a microhematocrit tube. Samples were kept on ice (up to 4 hours) until centrifugation. Samples were spun at 3000 x g (~5000 rpm) for 5 minutes and plasma was removed. Centrifuged plasma samples were kept on ice until they were frozen at -80 °C. Plasma samples were sent to the Northwest Fisheries Science Center in Seattle, WA where plasma IGF-1 concentrations were quantified by means of TRF-immunoassay, following the methods of Ferriss et al. (2014).

2.2.3 Statistical analysis

2.2.3.1 Differences in size and condition between spring thermal regimes

Sampling stations ranged from 59.98°N to 65.78° N and from -163.00°W to -172.00°W (Figure 2.1a). Prior to 2010, the number of stations within Norton Sound ranged from zero to three and there was a greater number of stations west of 189.00°W. Additionally, sampling in 2007 was generally restricted to the northern extent of the NEBS (Figure 2.1b). Due to these variations in sampling extent over the years, Norton Sound stations (i.e. east of -166.00°W), stations west of -171.00°W, and 2007 were dropped from our analysis of spring thermal regime effect on salmon size and condition. Years were classified as “warm” (2003-2005) or “cool” (2006-2007; 2009-2013) based on positive or negative May SST anomalies (hereafter referred to as “spring thermal regime”) in the SEBS, as documented in Farley et al. (2009) and depicted in Figure 1.1.

Mixed-effects models (Zuur et al. 2009) were used to determine if juvenile salmon size and condition in the NEBS significantly differed between SEBS spring thermal regimes. Separate analyses were run for each response variable (length, weight-length residuals, and energy density) and species. Models included spring thermal regime, Julian day, and length as fixed effects. For all analyses, we tested for an interaction between Julian day and spring thermal regime to evaluate whether growth rate differed between spring thermal regimes. Length was included as a covariate in the energy density models as it has been shown to correlate strongly with energy density in juvenile salmon (Andrews et al. 2009). To achieved normality, juvenile salmon calories/g and lengths were natural log-transformed. To account for random variation between years and possible pseudo-replication, station nested within year was included as a random effect. All statistical analyses were run using the open source statistical program R (R Core Team 2013).

2.2.3.2 Relationships between environmental variables and size, condition, and growth

Mixed-effects models (Zuur et al. 2009) were used to determine relationships between environmental variables and size, condition, and growth of juvenile chum and pink salmon. Separate analyses were run for each response variable (length, weight-length residuals, and energy density) and species. Full models included year, Julian day, sea surface temperature (SST), sea surface salinity (SSS), depth, and length (in energy density and pink salmon IGF-1 models) as fixed effects (Table 2.1). Year was included to account for inter-annual variability and Julian day was included to account for effects of growth over the duration of the surveys (Andrews et al. 2009).

Table 2.1 Full models of juvenile salmon response against environmental predictor variables. Models including chlorophyll-a were only tested on a subset of data that included chlorophyll-a.

Chum Salmon		
Response	**Fixed Effects**	**Random Effect**
Length	Year * Julian + SST + SSS + Depth	Station
Weight-length residual	Year * Julian + SST + SSS + Depth	Station
Energy Density	Year + ln(Length) + Julian day + SST + SSS + Depth (+ Chl-a)	Station
IGF-1	Year + Julian day + SST + Depth	Station
Pink Salmon		
Response	**Fixed Effects**	**Random Effect**
Length	Year * Julian + SST + SSS + Depth (+ Chl-a)	Station
Weight-length residual	Year * Julian + SST + SSS + Depth	Station
Energy density	Year + ln(Length) + Julian day + SST + SSS + Depth (+ Chl-a)	Station
IGF-1	Year + Length + SST + Depth	Station

Preliminary analyses (data not shown) were run with each response to determine whether station or a nested Julian day by station by year effect should included as the random effect and whether an interaction term between year and Julian day should be included in the full candidate models to account for differences in growth rate among years. Variation in length and weight-length residuals was best explained by the interaction between year and Julian day. In energy density models, length was included as a covariate and calories/g and length were natural log-transformed in order to achieve normality. Julian day best accounted for growth of juvenile chum salmon in IGF-1 models, while length best accounted for growth of juvenile pink salmon in IGF-1 models. For all models, station was included as a random effect to account for possible pseudoreplication.

We assessed multi-collinearity among environmental variables using Pearson's correlation tests. Only SST and SSS from stations where juvenile chum salmon were sampled for IGF-1 were highly correlated (correlation estimate = -0.67, p-value = 2.2e-16). Previous studies have shown temperature to be strongly correlated with growth and IGF-1 concentration (Larsen et al. 2001; Beckman et al. 2004c); therefore, SST was used in the models. SST and SSS have direct and indirect effects on salmon physiology that influence condition of juvenile salmon (Morita et al. 2001; Andrews et al. 2009; Heintz et al. 2013). In addition, SST and SSS also characterize water masses of the currents that flow through the NEBS (Eisner et al. 2012). Warmer and less saline water are characteristic of the Alaska Coastal Current (ACC) that flows northward along the coast of Alaska. As distance from shore increases, water temperatures tend to decrease and salinity increases, characteristic of the Bering Shelf Water (BSW). Bottom depth was included as a proxy for distance from shore, which provides information on how long a fish may have been in the marine environment (Bi et al. 2007, 2011; Burke et al. 2013).

Separate analyses were run for each response variable (length, weight-length residual, energy density, and IGF-1 concentration) and each species. Candidate models were determined a priori and all combinations of predictor variables were assessed.

2.2.3.3 Model selection

Candidate models describing relationships of juvenile salmon size (length), condition (weight-length residuals and energy density), and growth (IGF-1 concentration) with environmental factors were compared using an information-theoretic (I-T) model selection approach (Burnham and Anderson 2002). The benefit of this approach allows candidate models to be evaluated based on Akaike's information criterion (AIC) and Akaike weight (w_i) (Burnham and Anderson 2002; Hobbs and Hilborn 2006). Additionally, using an I-T model selection approach allows for an evaluation of individual predictor variables by their parameter weight (Burnham and Anderson 2002; Arnold 2010).

Akaike's information criterion bias-corrected for small sample size (AICc) was used to compare candidate models. Models with the lowest AICc value are considered to best represent the data. To compare models, ΔAICc was calculated for each model as the difference of its AICc from the lowest AICc. However, models with ΔAICc within 2 of the minimum AICc are often considered equivalent (Burnham and Anderson 2002). Biological inferences were drawn from the set of best models ($\Delta AICc \leq 2$) and importance of predictor variables was evaluated by their parameter weights (Burnham and Anderson 2002; Arnold 2010). In addition to ΔAICc and predictor variable parameter weight, we used Akaike weight (w_i) to evaluate sets of best models (Johnson and Omland 2004).

2.2.3.4 The addition of chlorophyll-a as a predictor variable

Chlorophyll-a levels were used as measure of primary production, giving information on energy available to higher trophic levels (Brodeur et al. 2004; Bi et al. 2007, 2011; Peterson et al. 2010; Burke et al. 2013). However, chlorophyll-a was included in a separate analysis because only a subset of stations had chlorophyll-a data. Candidate models describing relationships between salmon size, growth, and condition and environmental variables were assessed using AICc, as described above.

2.3 Results

2.3.1 Variation in station location and survey timing

There was variation in timing and location of sampling within the NEBS (Figures 2.1 and 2.2). Prior to 2010, Norton Sound was not extensively sampled and there was a greater number of stations west of -166.00°W, and in 2007 only the most northern portion of the NEBS was heavily sampled (Figure 2.1b). Excluding 2007, there was a slight northward and pronounced eastward/onshore shift in the average station location over the time period of the study (Figure 2.2a,b). There were annual differences in juvenile chum and pink salmon distribution (Figure 2.2). While both species showed similarity in latitudinal range, pink salmon were generally sampled at stations further offshore (at stations with a more negative longitude) and at stations with deeper bottom depths (Figure 2.2b,c).

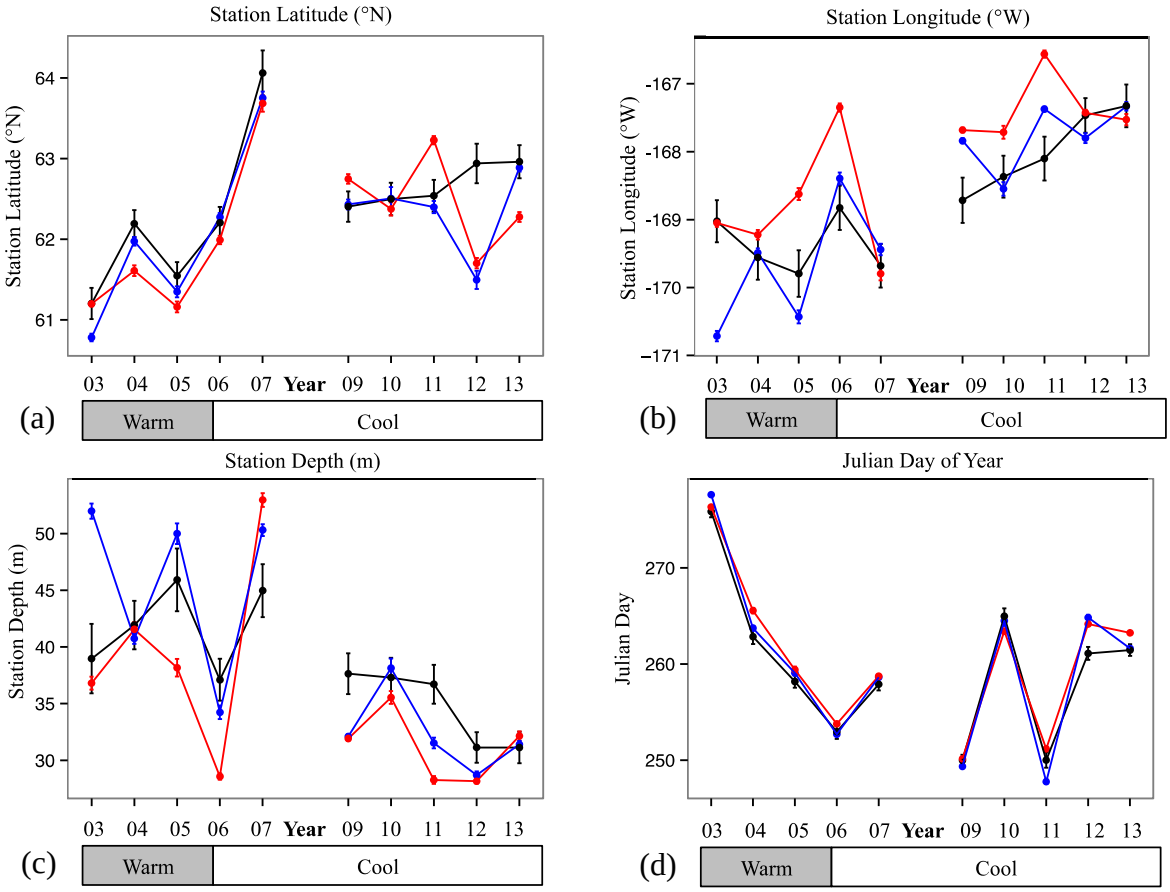


Figure 2.2 Differences in station location and sampling time between 2003-2007 and 2009-2013 from all stations (Black), stations where chum salmon present (Red), and stations where pink salmon present (Blue). (a) Mean station latitude, (b) mean station longitude, (c) mean station depth, and (d) mean Julian day of sampling. Bars indicate spring thermal regime.

2.3.2 Differences in size and condition between spring thermal regimes

To account for variability in survey design among years, stations within Norton Sound, stations west of -171.00°W, and all stations in 2007 were removed from analyses testing for differences in salmon response between spring thermal regimes, but included in all other analyses. In analyses of length of chum and pink salmon by spring thermal regime, there was a significant interaction between Julian day and spring thermal regime. Length was significantly greater during the warm regime for both species (Figure 2.3a; Table 2.2). There were no significant differences in weight-length residuals between regimes in the NEBS for either species (Figure 2.3b; Table 2.2). Energy density of chum and pink salmon was significantly reduced during warm years (Figure 2.3c; Table 2.2).

2.3.3 Environmental variables across stations in relation to where salmon were caught

Generalized additive models (GAMs) were used to plot SST, SSS, and bottom depth gradients within the NEBS from our dataset. Results from GAMs reflect a general cooling in SST and gradual increases in SSS and bottom depth with distance from shore (Figure 2.4).

SST, SSS, and chlorophyll-a levels varied among years at survey stations (Figure 2.5). There was a general decrease in SST and SSS in the NEBS over the survey years (Figure 2.5a). In 2006, there were distinct declines in SSS and chlorophyll-a levels (Figure 2.5b,c). Decreases in SSS may be a consequence of the shift from offshore to near-shore sampling in study design between years (Figure 2.3b,c). Chlorophyll-a levels were highly variable between years (Figure 2.5c). Compared to juvenile pink salmon, juvenile chum salmon were found in warmer, shallower, and less saline waters, with higher levels of chlorophyll-a, illustrating their tendency to be caught closer to shore (Figure 2.5).

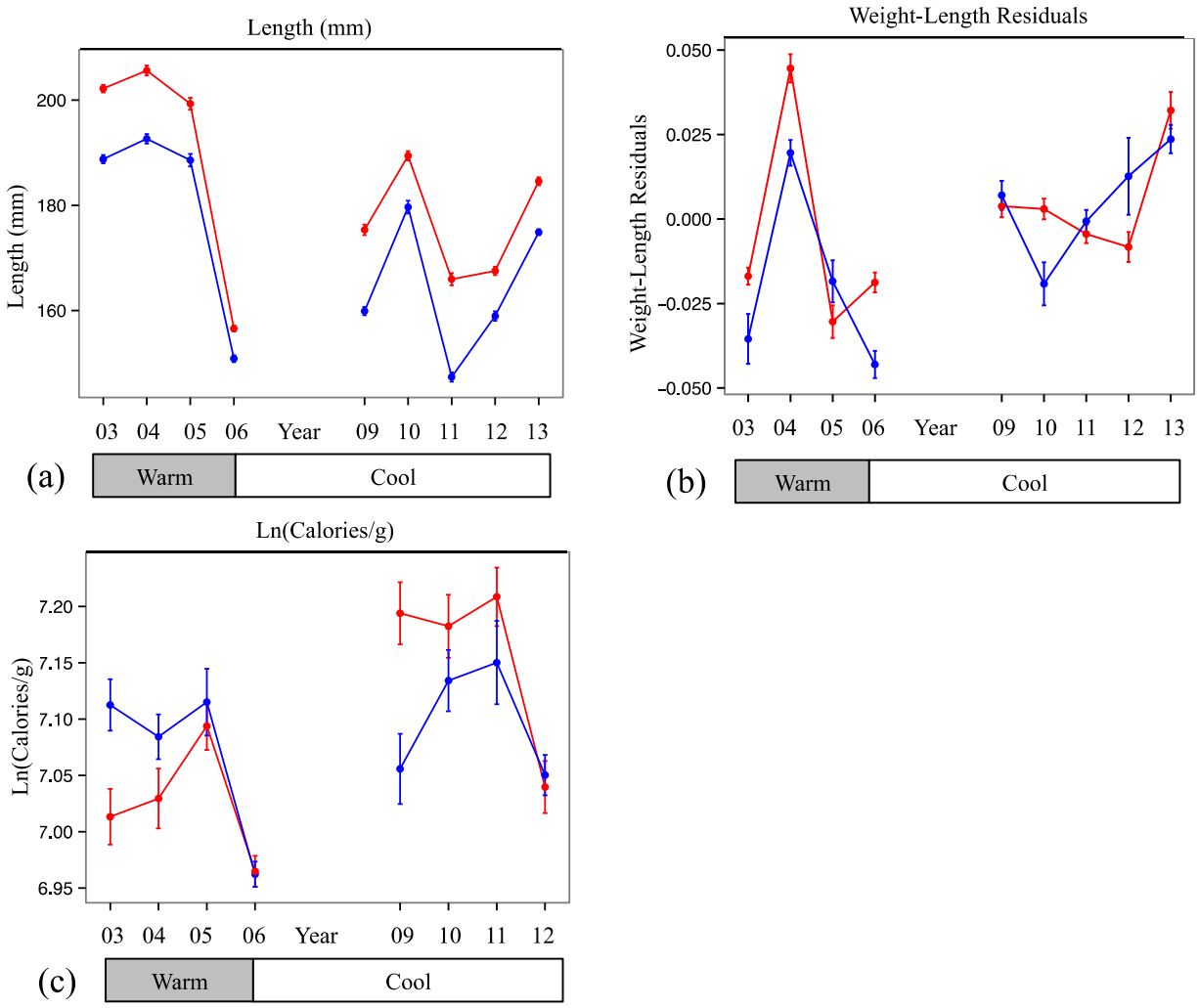


Figure 2.3 Juvenile chum (Red) and pink salmon (Blue) physiological measures from stations west of -166°W and east of -171°W, collected from 2003-2006 and 2009-2013. (a) Salmon length (mm), (b) salmon weight-length residuals, and (c) salmon ln (calories/g), no data available for 2013. Bars indicate spring thermal regime.

Table 2.2 Coefficients from juvenile salmon models evaluating variation in physiological responses related to spring thermal regime. Random effects include standard deviation of salmon response between years (A), between stations (B), and within stations (C). Values in parentheses are standard deviations.

Chum Salmon			**Fixed Effects**				**Random Effects**		
Response	**Intercept**	**Warm Regime**	**Julian day**	**Julian *Regime**	**ln(Length)**	**Regime P-value**	**σ^2A**	**σ^2B**	**σ^2C**
Length (mm)	-326.916 (64.173)	425.384 (105.870)	1.949 (0.248)	-1.563 (0.402)	NA	0.005	10.370	12.497	12.030
Weight-length residual	-0.008 (0.010)	-0.001 (0.017)	NA	NA	NA	0.994	0.022	0.046	0.062
Energy density (ln(calories/g))	2.908 (0.290)	-0.130 (0.026)	NA	NA	0.808 (0.056)	0.002	0.030	2.78e-6	0.083

Pink Salmon			**Fixed Effects**				**Random Effects**		
Response	**Intercept**	**Warm Regime**	**Julian day**	**Julian *Regime**	**ln(Length)**	**Regime P-value**	**σ^2A**	**σ^2B**	**σ^2C**
Length (mm)	-162.383 (56.094)	315.624 (92.89)	1.261 (0.218)	-1.130 (0.354)	NA	0.012	4.494	12.138	11.597
Weight-length residual	-0.008 (0.009)	-0.009 (0.015)	NA	NA	NA	0.578	0.017	0.049	0.072
Energy density (ln(calories/g))	3.352 (0.281)	-0.057 (0.022)	NA	NA	0.726 (0.055)	0.043	0.015	0.068	0.059

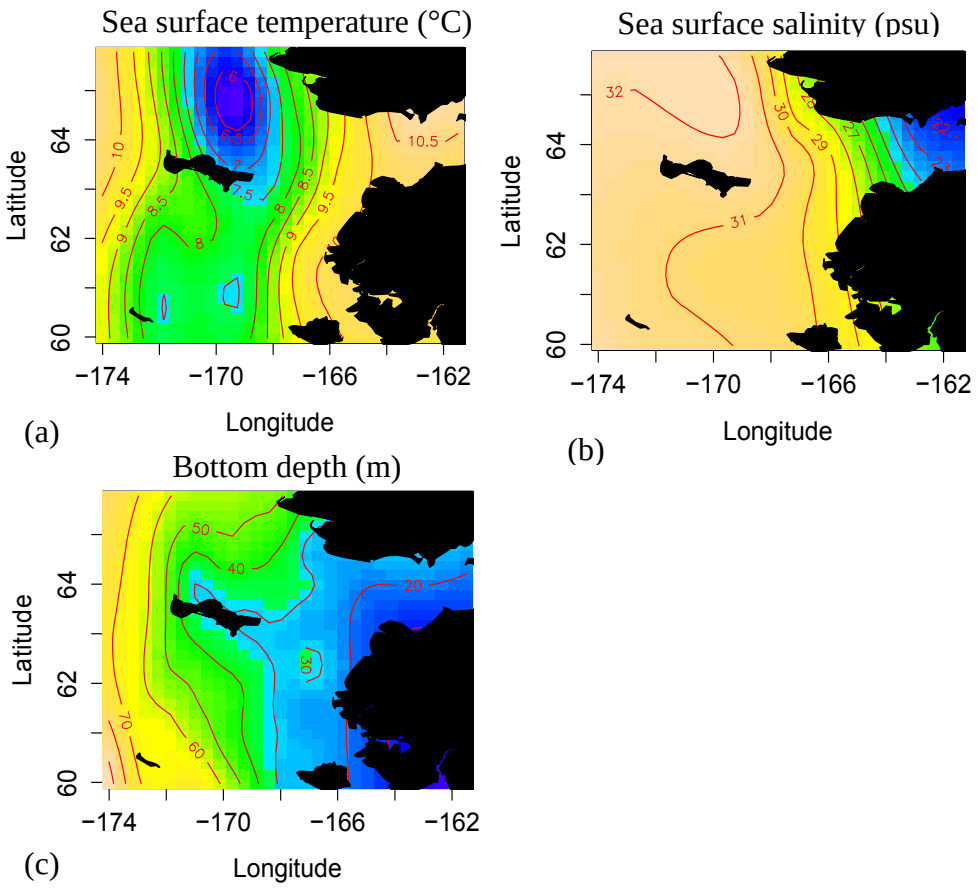


Figure 2.4 Plots from generalized additive models, using data from all years (2003-2007; 2009-2013) of (a) Sea surface temperature versus latitude and longitude, (b) sea surface salinity versus latitude and longitude, and (c) depth versus latitude and longitude.

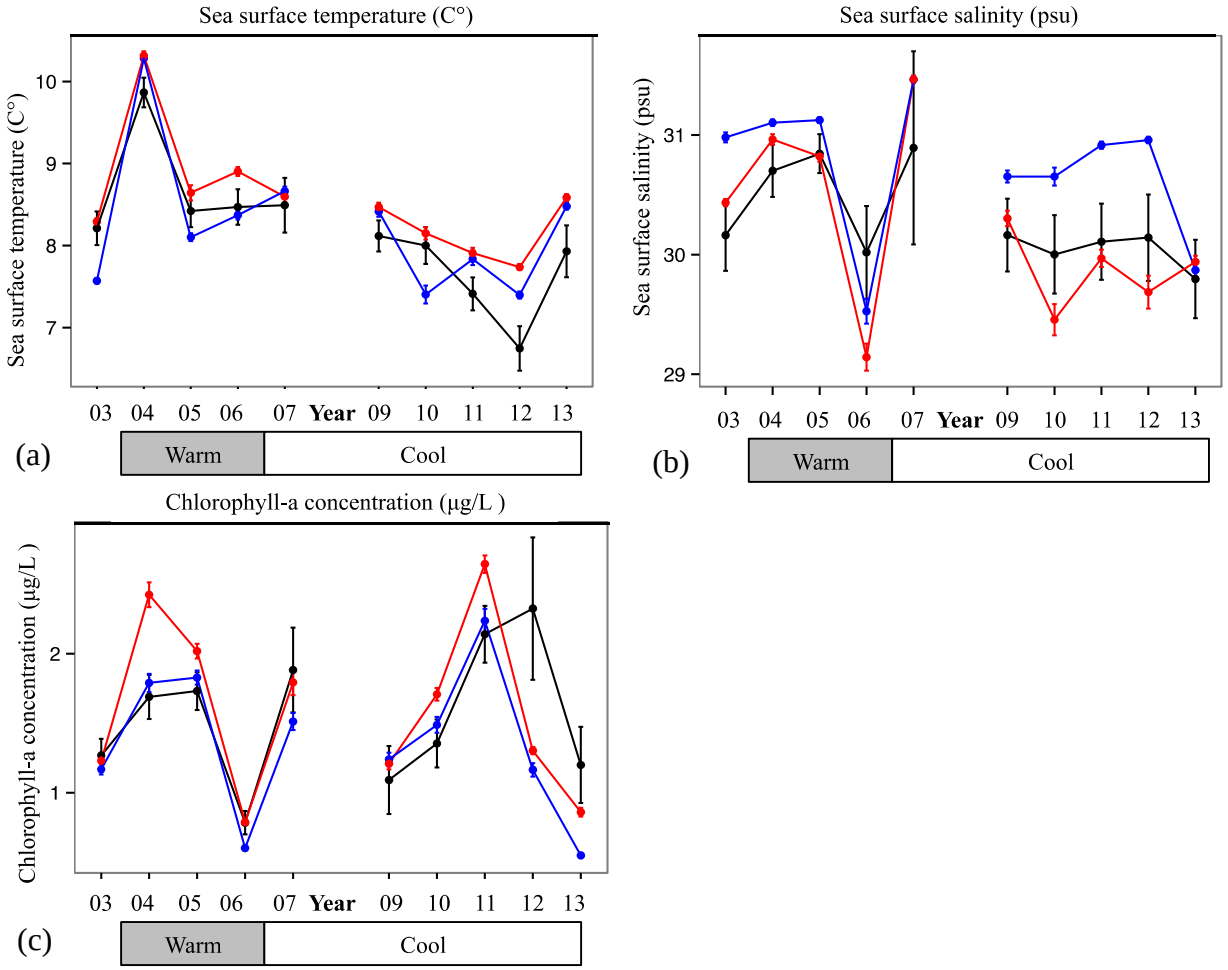


Figure 2.5 Plots of environmental variables from all stations sampled between 2003-2007 and 2009-2013. Average values from all stations (Black), stations where chum salmon present (Red), and stations were pink salmon were present (Blue). (a) Sea surface temperature (°C), (b) sea surface salinity (psu), and (c) chlorophyll-a concentration (µg/L). Bars indicate spring thermal regime.

2.3.4 Relationships between length and environmental variables

Models with ΔAICc ≤ 2 indicated that length of both chum and pink salmon was negatively associated with SST and positively associated with Julian day, SSS, and depth (Table 2.3; Table 2.4). The Akaike weights of length models with a ΔAICc of 0 were greater than models within ΔAICc ≤ 2, suggesting that depth and SST were the most important explanatory variables of juvenile salmon length (Table 2.3; Table 2.4). The low parameter weight of SSS provided support for its exclusion from models (Table 2.5).

2.3.5 Relationships between weight-length residuals and environmental variables

Models with ΔAICc ≤ 2 indicated that weight-length residuals in both species were negatively associated with depth, SSS, and Julian day, and positively associated with SST (Table 2.3; Table 2.4). Akaike weights of models with the lowest AICc suggested that depth and SST were the most important explanatory variables for juvenile chum salmon weight-length residuals and depth was an important explanatory variable for juvenile pink salmon weight-length residuals (Table 2.3; Table 2.4). Parameter weight of SSS was considerably lower than the other explanatory variables, providing support for its exclusion from models (Table 2.5). Additionally, the low parameter weight of SST provides support for its exclusion from the pink salmon weight-length residual model (Table 2.5).

2.3.6 Relationships between energy density and environmental variables

Models with ΔAICc ≤ 2 indicated energy density was negatively associated with SST in both species (Table 2.3; Table 2.4). SSS was negatively associated with chum salmon energy density and positively associated with pink salmon energy density (Table 2.3; Table 2.4).

Table 2.3 Model coefficients and Akaike weights of chum salmon models with ΔAICc ≤ 2. Random effects include standard deviation of salmon response between stations (A), and within stations (B). A dash indicates that explanatory variable was not included in models with ΔAICc ≤ 2, and 'NA' indicates that the explanatory model was not included in the full candidate model. Value in parenthesis is standard deviation.

Chum Salmon			**Fixed Effects**						**Random Effects**	
Response	**ΔAICc**	**W_i**	**Intercept**	**SST**	**SSS**	**Depth**	**Julian day**	**Length**	**σ^2A**	**σ^2B**
Length	0	0.42	-551.299 (195.878)	-4.157 (0.686)	---------	0.139 (0.074)	2.827 (0.705)	NA	11.641	12.419
Length	0.92	0.27	-608.744 (204.165)	-3.644 (0.857)	0.565 (0.566)	0.133 (0.075)	2.958 (0.717)	NA	11.642	12.419
Length	1.76	0.18	-515.299 (195.964)	-4.711 (0.622)	---------	---------	2.734 (0.707)	NA	11.710	12.419
Weight-length residual	0	0.40	-0.404 (0.699)	0.005 (0.002)	---------	-0.001 (0.001)	-0.001 (0.003)	NA	0.039	0.061
Weight-length residual	1.98	0.15	-0.359 (0.731)	0.005 (0.003)	-0.001 (0.002)	-0.001 (0.001)	-0.001 (0.003)	NA	0.040	0.061
Energy Density	0	0.70	4.916 (0.501)	-0.016 (0.005)	-0.009 (0.003)	---------	-0.007 (0.002)	0.854 +/- 0.051	0.032	0.078
IGF-1	0	0.49	141.411 (26.291)	1.355 (0.324)	NA	---------	-0.437 (0.102)	NA	2.372	6.664
IGF-1	0.05	0.48	158.739 (29.196)	1.063 (0.389)	NA	-0.071 (0.053)	-0.487 (0.109)	NA	2.367	6.658

Table 2.4 Model coefficients and Akaike weights of pink salmon models with ΔAICc ≤ 2. Random effects include standard deviation of salmon response between stations (A), and within stations (B). A dash indicates that explanatory variable was not included in models with ΔAICc ≤ 2, and 'NA' indicates that the explanatory model was not included in the full candidate model. Value in parenthesis is standard deviation.

Pink Salmon			**Fixed Effects**						**Random Effects**	
Response	**ΔAICc**	**W_i**	**Intercept**	**SST**	**SSS**	**Depth**	**Julian day**	**Length**	**σ^2A**	**σ^2B**
Length	0	0.72	-126.993 (37.442)	-2.702 (0.730)	----	0.277 (0.070)	1.179 (0.130)	NA	10.118	12.535
Length	1.98	0.27	-132.821 (48.340)	-2.616 (0.859)	0.140 (0.734)	0.275 (0.071)	1.182 (0.132)	NA	10.144	12.535
Weight-length residual	0	0.40	-0.917 (0.884)	--------	---------	-0.001 (0.001)	0.003 (0.003)	NA	0.045	0.073
Weight-length residual	1.26	0.21	-1.098 (0.910)	0.003 (0.003)	---------	-0.001 (0.001)	0.004 (0.003)	NA	0.045	0.073
Weight-length residual	1.55	0.19	-0.845 (0.891)	---------	-0.002 (0.003)	-0.001 (0.003)	0.003 (0.003)	NA	0.045	0.073
Energy Density	0	0.28	5.265 (0.574)	-0.010 (0.006)	---------	---------	-0.007 (0.002)	0.755 (0.049)	0.058	0.062
Energy Density	0.9	0.18	4.754 (0.493)	---------	---------	---------	-0.006 (0.002)	0.775 (0.048)	0.059	0.062
Energy Density	1.47	0.14	4.731 (0.493)	---------	0.006 (0.005)	---------	-0.007 (0.002)	0.764 (0.048)	0.059	0.062
Energy Density	1.630	0.13	5.070 (0.629)	-0.011 (0.006)	---------	-0.001 (0.001)	-0.007 (0.002)	0.760 (0.049)	0.058	0.062
IGF-1	0	0.35	-18.787 (23.468)	1.521 (0.545)	0.927 (0.656)	0.102 (0.062)	NA	0.092 (0.037)	1.779	5.953
IGF-1	0.51	0.27	11.887 (9.012)	1.172 (0.494)	----	0.099 (0.063)	NA	0.094 (0.037)	1.859	5.957
IGF-1	1.78	0.14	16.008 (8.812)	0.990 (0.504)	----	------	NA	0.099 (0.037)	2.112	5.939

Table 2.5 Predictor parameter weights from models of juvenile salmon response variables against environmental variables.

Species	Response	SST	SSS	Depth	Julian day	Length
Chum Salmon	Length	1	0.40	0.69	1	NA
	Weight-length residual	0.76	0.40	0.77	1	
	Energy density	0.95	0.91	0.25	1	1
	IGF-1	0.97	NA	0.51	1	NA
Species	**Response**	**SST**	**SSS**	**Depth**	**Julian day**	**Length**
Pink Salmon	Length	1	0.27	1	1	NA
	Weight-length residual	0.33	0.32	1	1	
	Energy density	0.42	0.28	0.66	1	1
	IGF-1	0.85	0.44	0.75	NA	0.86

Depth was negatively associated with pink salmon energy density (Table 2.4). However, the low parameter weights of SSS and depth from the pink salmon models provided evidence for their exclusion from models (Table 2.5).

2.3.7 Relationships between IGF-1 concentration and environmental variables

Models with $\Delta AICc \leq 2$ indicated IGF-1 concentrations were positively associated with SST (Table 2.3; Table 2.4). Depth was negatively associated with chum salmon IGF-1 concentration (Table 2.3). Salinity and depth were positively associated with pink salmon IGF-1 concentration (Table 2.4). Juvenile chum salmon IGF-1 concentration models with the highest Akaike weights differed only in their inclusion of depth, suggesting both models adequately described chum salmon IGF-1 concentration (Table 2.3). The exclusion of depth is supported by its low parameter weight (Table 2.5). Juvenile pink salmon IGF-1 concentration models with the highest Akaike weights differed by the inclusion of SSS (Table 2.4). The low parameter weight of SSS provided support for its exclusion from the model (Table 2.5).

IGF-1 concentrations of both species were greater in 2010-2012, compared to 2009 (Figure 2.6a). Additionally, mean IGF-1 concentration of juvenile chum salmon sampled within Norton Sound was greater than the rest of the NEBS region (Figure 2.6b).

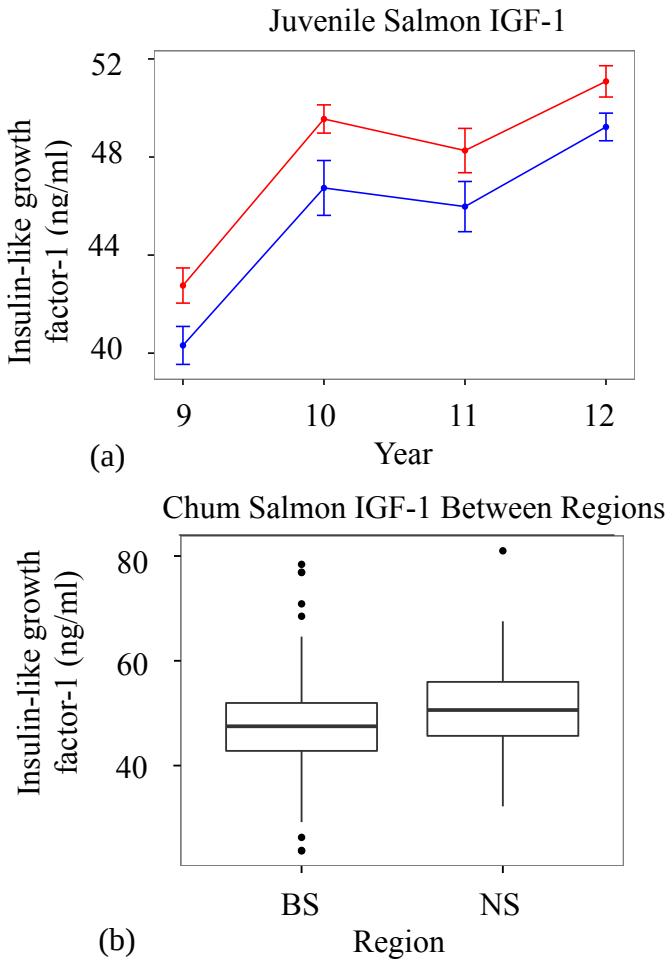


Figure 2.6 Plots showing IGF-1 concentration overtime and differences between Norton Sound and Bering Sea. (a) Chum (Red) and pink salmon (Blue) IGF-1 concentration from 2009-2012. (b) Boxplots of juvenile chum salmon showing median, interquartile range, and individuals outside interquartile range of IGF-1 concentrations between the Bering Sea (BS; N=379) and Norton Sound (NS; N=94).

2.3.8 Inclusion of Chlorophyll-a

There was a negative relationship between chlorophyll-a and juvenile pink salmon length (Table 2.6). However, Akaike weights of pink salmon length models with and without chlorophyll-a were essentially equal (Table 2.6). Furthermore, exclusion of chlorophyll-a was supported by its low parameter weight (Table 2.7). Juvenile salmon energy density was positively associated with chlorophyll-a (Table 2.6). Akaike weights strongly supported inclusion of chlorophyll-a in the juvenile chum salmon energy density model (Table 2.6). Both the Akaike weights and the parameter weight of chlorophyll-a indicated the additional explanatory power of chlorophyll-a in juvenile pink salmon energy density model (Table 2.6; Table 2.7).

2.4 Discussion

2.4.1 Differences in size and condition between spring thermal regimes

Larger sized salmon often have increased marine survival during their first year at sea (Beamish and Mahnken 2001; Farley et al. 2007; Moss et al. 2009) and it has been presumed that larger salmon would have greater lipid reserves needed to survive their first winter at sea (Beamish and Mahnken 2001; Farley and Trudel 2009). Andrews et al. (2009) compared juvenile pink salmon length and condition in the NEBS among years with warm (2004 and 2005) and cool (2006 and 2007) spring and summer SSTs and found that juvenile pink salmon were longer, but of reduced condition during warm years. Our findings of increased length of juvenile chum and pink salmon during the warm spring thermal regime and increased energy density during the cool spring thermal regime support those of Andrews et al. (2009).

Table 2.6 Models with chlorophyll-a were only shown in tables if the inclusion of chlorophyll-a improved model fit. Model coefficents and Akaike weights of models with ΔAICc ≤ 2 from models including chlorophyll-a. Random effects include standard deviation of salmon response between stations (A), and within stations (B). Value in parenthesis is standard deviation.

Chum Salmon						**Fixed Effects**				**Random Effects**	
Response	**ΔAICc**	**W_i**	**Intercept**	**SST**	**SSS**	**Depth**	**Chl-a**	**Julian day**	**Length**	**σ^2A**	**σ^2B**
Energy Density	0	0.81	4.913 (0.507)	-0.016 (0.005)	-0.009 (0.003)	NA	0.010 (0.004)	-0.007 (0.002)	0.856 (0.050)	0.032	0.076
Pink Salmon						**Fixed Effects**				**Random Effects**	
Response	**ΔAICc**	**W_i**	**Intercept**	**SST**	**SSS**	**Depth**	**Chl-a**	**Julian day**	**Length**	**σ^2A**	**σ^2B**
Length	0	0.49	75.718 (194.262)	-2.979 (0.771)	NA	0.287 (0.073)	-1.130 (0.782)	0.457 (0.698)	NA	10.237	12.658
Length	0.14	0.45	59.632 (194.927)	-2.834 (0.768)	NA	0.289 (0.073)	----------	0.505 (0.700)	NA	10.300	12.657
Energy Density	0	0.26	4.833 (0.501)	----------	NA	----------	0.012 (0.006)	-0.007 (0.002)	0.775 (0.048)	0.058	0.061
Energy Density	0.82	0.21	5.238 (0.580)	-0.008 (0.006)	NA	----------	0.011 (0.006)	-0.007 (0.002)	0.759 (0.049)	0.058	0.061
Energy Density	1.75	0.12	5.000 (0.632)	-0.009 (0.006)	NA	-0.001 (0.001)	0.012 (0.006)	-0.007 (0.002)	0.766 (0.049)	0.058	0.061

Table 2.7 Predictor parameter weights from models of juvenile salmon response variables and environmental variables, including chlorophyll-a.

Species	Response	SST	SSS	Depth	Chl-a	Julian day	Length
Chum Salmon	Energy density	0.97	0.94	NA	0.88	1	1
Species	**Response**	**SST**	**SSS**	**Depth**	**Chl-a**	**Julian day**	**Length**
Pink Salmon	Length	0.94	NA	0.94	0.49	1	NA
	Energy density	0.52	NA	0.31	0.73	1	1

While we found juvenile salmon in the NEBS were longer during the warm regime and more energy dense during the cool regime, there were no significant differences in weight-length residuals between regimes. Weight-length residuals do not provide any information on body composition, and may not be an adequate measure of condition when comparing between warm and cool regimes. These results may reflect real differences in the effect of spring thermal regime in the SEBS on energy allocation and length between species in the NEBS. However, salmon responses were highly variable between years within both spring thermal regimes (Figure 2.3), suggesting that differences in salmon size and energy density in the NEBS cannot be attributed to spring thermal regime alone.

Previous studies have highlighted interactions between pink salmon and other species of salmon (Azumaya and Ishida 2000; Ishida et al. 2002; Ruggerone et al. 2010; Ruggerone et al. 2012; Agler et al. 2013; Kaga et al. 2013). While our study did not directly address issues of competition between pink and chum salmon, we did observe similar trends in size and condition over time, suggesting that both species respond in similar ways to ocean condition (Figure 2.3). However, while juvenile salmon responses were generally similar over time, there were some interesting differences. There was a decrease in juvenile pink salmon weight-length residuals from 2009 to 2010, while juvenile chum salmon weight-length residuals remained similar (Figure 2.3b). An opposite trend was observed between 2010 and 2011, where juvenile chum salmon weight-length residuals decreased and pink salmon weight- length residuals increased (Figure 2.3b). Variability of weight-length residuals between species corresponded to variability in sampling date and changes in distribution over time (Appendices I, II, and III). For example, pink salmon were captured further offshore in 2010, compared to 2009 (Figure 2.2b), and this increase in offshore distribution of pink salmon may have contributed to differences in weight-

length residuals between years. Additionally, these trends are likely influenced by variability in mean Julian day of sampling between 2009 and 2011 (Figure 2.2d). The earlier mean sampling date of 2009 and 2011 may correspond more closely with ocean entry date for juvenile pink salmon, reflected by the greater weight-length residuals of juvenile pink salmon in 2009 and 2011. Conversely, the later mean sampling date of 2010 may correspond more closely with ocean entry date for juvenile chum salmon.

Second, juvenile chum energy density was less than pink salmon during years within the warm spring thermal regime of the SEBS (2003-2005), but greater than pink salmon energy density during years within the cool spring thermal regime of the SEBS (2006-2007; 2009-2013; Figure 2.3c). These results suggest spring thermal regime of the SEBS may be a good indicator of conditions in the NEBS that are directly affecting juvenile chum salmon. For example, juvenile chum salmon are distributed more nearshore, within the Alaska Coastal Current (ACC) water, compared to pink salmon. The ACC is characterized as warmer, less saline, and more nutrient limited compared to the offshore, Bering Shelf Water (BSW). Additional warming during the warm thermal regime may have contributed to the reduced condition of juvenile chum salmon within the warm regime.

2.4.2 Relationships between physiological measures and environmental variables

Contrary to our hypothesis that length would be positively related to SST, our models indicated that greater length was associated with cooler SSTs and deeper bottom depths. While our models reflected within and among year relationships between salmon physiological measures and environmental variables, it is likely that the offshore movement of fish as they grow drove the relationships between length and environmental variables, with larger fish being caught at stations with cooler SSTs and deeper bottom depths.

Juvenile salmon are thought to experience two major periods of mortality during their first marine year. The first is well documented and is related to size-selective predation early in marine life (Parker 1968; Pearcy 1992). The second relates to a period of natural mortality experienced in the fall and winter because juvenile salmon have not stored the fat reserves necessary to maintain minimum metabolic requirements (Beamish and Mahnken 2001). Therefore, throughout the summer and into fall, juvenile salmon must allocate energy to length and fat storage. Our results suggest that over the course of the survey, juvenile salmon may be allocating more energy to length. Juvenile salmon sampled close to shore (shallower bottom depth) weighed more for a given length than those sampled further offshore. In addition, the negative relationship between Julian day and weight-length residuals reflect that fish sampled earlier in the surveys weighed more for a given length. However, Julian day was included in our models in order to account for interannual variability in survey design of the years. Therefore true relationships between Julian day and juvenile salmon physiological measures may not be reflected by our results.

The negative relationship between energy density and temperature are in agreement with lab studies showing cooler temperatures facilitate greater energy storage in juvenile coho salmon, regardless of diet (Heintz 2009). However, the relationship between cooler SST and increased energy density may have reflected changes in oceanography within and between water masses in the NEBS. In our study, juvenile chum and pink salmon were caught within the two major currents of the NEBS, the ACC and BSW. It is likely that nearshore stations correspond to the ACC, while offshore stations correspond to the BSW. The warm waters of the ACC are nutrient-limited in the summer (Grebmeier et al. 2006b). Cooler SSTs in this region may be associated with wind mixing events that increase the amount of production in the water column,

providing resources to higher trophic levels (Ladd and Stabeno 2012). Furthermore, cooler SSTs of the BSW are associated with higher densities of lipid-rich species of zooplankton (Richardson 2008; Hunt et al. 2011; Eisner et al. 2012; Stabeno et al. 2012a). Thus, in addition to the physiological relationship between cooler SSTs and energy density, cooler SSTs may serve as an indicator for higher ocean productivity. Future studies in the NEBS should incorporate zooplankton composition and juvenile salmon diet to determine the mechanisms driving relationships between temperature, zooplankton composition, and energy density.

Our results found juvenile salmon IGF-1 concentration to be positively related to SST. Between 2009 and 2012, 2009 experienced the highest average SST but the lowest concentrations of juvenile salmon IGF-1 (Figures 2.5a and 2.6a). These results may be a consequence of differences in sampling extent between years. For example, Norton Sound was sampled more extensively sampled in 2010-2012, compared to 2009. Mean IGF-1 concentration of juvenile chum salmon sampled within Norton Sound was greater than the rest of the NEBS region (Figure 2.6b). High IGF-1 concentration may be an indicator of prey availability, as growth can only occur if nutritional needs are met (Beckman 2011). Thus, these results may reflect differences in food availability between Norton Sound and the rest of the NEBS region. However, factors such as quality and quantity of prey, distribution and overlap of salmon and prey, and SST effects on prey field and salmon metabolism influence IGF-1 concentration. Thus, it is likely a combination of multiple factors contributed to improved growth between 2010 and 2012. Overall, IGF-1 concentration between 2009 and 2012 suggests that conditions in the NEBS region support growth of juvenile chum and pink salmon.

Chlorophyll-a was important for explaining the variability in energy density for both species. Higher energy density was associated with higher chlorophyll-a concentration and

cooler SSTs, supporting our earlier speculation that cooler SSTs would indicate increased productivity and enhanced feeding success at higher trophic levels. This inference is supported by previous studies using chlorophyll-a levels as a measure of energy available to higher trophic levels (Brodeur et al. 2004; Bi et al. 2007, 2011; Peterson et al. 2010; Burke et al. 2013). Additionally, higher chlorophyll-a concentrations may be an indicator of the more productive BSW.

All three measures of juvenile salmon size and condition responses were diminished in 2006. While 2006 is considered a cool year based on spring thermal regime in the SBS, ice extent in the Bering Sea during this year was comparable to years of the warm spring thermal regime (Stabeno et al. 2012b). Cooper et al. (2006) pointed out that winds can have a strong influence on water masses in the NEBS region. In 2006, strong easterly and northeasterly winds may have spread the ACW further offshore, contributing to the large influence of the fresh, nutrient poor waters of the ACW in the NEBS (Cooper et al. 2012). In addition, Cooper et al. (2012) found reduced winter brine formation in 2006, a consequence of reduced sea ice, and the authors suggested this might have limited nutrient availability within the NEBS. Our results showing reduced chlorophyll-a and salinity in 2006 support these findings (Figure 2.5b,c).

Bathymetry and ocean current characterization suggest SST, SSS, and depth gradients exist within the NEBS, with SST decreasing with distance from shore and SSS and depth increasing. Generalized additive models (GAMs) were used to plot SST, salinity, and bottom depth gradients within the NEBS from our data. Results confirm a general gradual cooling in SST, gradual increases in salinity and bottom depth with distance from shore (Figure 2.4). However, model results show the region above Saint Lawrence Island, known as Chirikov Basin, as being generally cooler, more saline, and having deeper bottom depths. Thus, the east to west

gradients of SST, SSS, and depth are confounded by characterization of the Chirikov Basin. Furthermore, patterns in wind, weather, and seasonal sea ice extent and timing influence the distribution of currents within the NEBS, resulting in annual variation.

2.5 Conclusions

Our model results may reflect differences in energy allocation of juvenile chum and pink salmon in the NEBS between spring thermal regimes of the SEBS. However, our analysis of spring thermal regime effects was confounded by inter-annual variability in salmon size and condition (Figure 2.3) and was likely influenced by distribution differences (Figure 2.2). Furthermore, juvenile chum and pink salmon followed similar trends in size and condition between years, suggesting that both species respond similarly to changes in ocean condition (Figure 2.3). While we found salmon were longer during the warm thermal regime and more energy dense during the cool thermal regime, variability of physiological measures between years within thermal regimes suggest that differences in salmon size and condition in the NEBS cannot be attributed to spring thermal regime alone. Furthermore, the corresponding declines in physiological measures with salinity and chlorophyll-a concentration in 2006 provided evidence of additional processes that may influence size and condition of juvenile salmon within the NEBS.

The association between cooler SST with length may reflect the offshore movement of juvenile salmon as they grow larger. Additionally, the negative relationship between SST with length and energy density suggested the influence of indirect effects of SST on productivity and juvenile salmon condition in the NEBS. Cooler SST are indicative of upwelling events that serve to increase surface water nutrients, and may be an indicator of the more productive BSW.

Additionally, cooler SSTs tend to support larger and more nutrient rich prey sources. Increases in IGF-1 concentration from 2009 likely reflected a combination of factors such as prey quality and quantity, feeding success, and SST effects on prey field and salmon metabolism that contributed to improved growth between 2010 and 2012.

In conclusion, our results may reflect real differences in the effect of spring thermal regime in the SEBS on energy allocation and length of juvenile chum and pink salmon in the NEBS. Additionally, consistencies across physiological measures of juvenile salmon indicated that recent productivity levels of the NEBS region support juvenile chum and pink salmon growth and condition during their first marine summer. While current climate patterns have facilitated cooling temperatures in the NEBS, future decreases in seasonal sea ice and continued Arctic warming can be expected to have an effect on spring thermal regimes within the Bering Sea. The major declines in salmon physiological measures, salinity, and chlorophyll-a in 2006 corresponded to strong easterly and northeasterly winds, providing support for the strong effect of wind on water masses within the NEBS (Cooper et al. 2006, 2012). Furthermore, the negative correlation between SST and juvenile salmon energy density and length likely reflect the indirect effects of cooler SSTs on ecosystem dynamics. While temperature does serve to increase metabolic processes, warming SST may result in changes in ecosystem function, such as increased competition and changes in prey composition, that result in decreased growth and condition of juvenile salmon. Continued research in the NEBS is necessary in order to monitor how changes in climate are affecting commercially important species, such as salmon.

Chapter 3: Differences in growth and condition of juvenile pink (*Oncorhynchus gorbuscha*) salmon between even and odd brood years within the northeastern Bering Sea

3.1 Introduction

Among the different species of salmon, pink salmon have a unique two-year life cycle with even- and odd-year stocks (with 'even' and 'odd' referring to brood year) being genetically distinct (Apsinwall 1974; Beacham and Murray 1988; Beacham et al. 2012). The strong genetic separation between the two brood-years is likely a consequence of spatial separation during Pleistocene Era glaciation, with even stocks surviving in the north and odd stocks in the south (Aspinwall 1974). This separation during glaciation may explain the greater embryonic survival of the even stocks, compared to odd stocks, in cold (4°C) environments (Beacham and Murray 1988). The adaptability of the even stocks to cold environments is also reflected by the low even stock abundance in Washington, and their greater abundance relative to odd stocks in western Alaska (Ruggerone et al. 2003; Beacham et al. 2012).

While catches of Pacific salmon in the sub-Arctic have increased (Beamish 2012), our knowledge regarding how ocean conditions within the Arctic and sub-Arctic regions affect growth and condition of juvenile salmon remains limited. Pink salmon are one of the most northerly distributed species of Pacific salmon in Alaska (Irvine et al. 2009; Nielsen et al. 2012) and along with chum salmon make up 80% of all salmon catches in the sub-Arctic (Beamish 2012). Sub-Arctic and Arctic warming is likely to influence growth and condition of resident juvenile pink salmon inhabiting these regions in the future. While previous studies within the northeastern Bering Sea (NEBS) have shown differences in energy density of pink salmon between warm and cool years (Andrews et al. 2009), few studies have examined differences in

growth and condition between even and odd stocks of pink salmon (Beacham et al. 2012; Beamish 2012).

It has been speculated that genetic differences between even and odd stocks may include differences in metabolic strategy (Beamish 2012). The short life cycle of pink salmon has corresponded with the evolution of rapid marine growth (Ricker 1976; Brett 1979). Rapid growth of juvenile salmon is accomplished by high feeding rates, maintaining a full stomach at high prey densities (Godin 1981). In recent years, odd stocks of pink salmon in the Fraser River system, British Columbia, have increased, while even stocks have remained fairly constant (Beamish 2012). Beamish (2012) attributed this to differences in metabolic strategy during the first marine summer between stocks, with odd stocks allocating more energy to growing in length and even stocks allocating more energy to fat storage. This difference in energy allocation would allow odd stocks to benefit from the increased prey production during late fall that has been attributed to warming off the coast of British Columbia, and thus could explain why odd stocks have increased in abundance in that region while even stocks have not (Beamish 2012). In this study, we investigated even/odd differences in size, growth, and condition in pink salmon during their first summer in the NEBS, after accounting for inter-annual variability in environmental conditions influencing those parameters (Chapter 2).

We used several indices to assess size, condition, and growth including length, weight-length residuals, energy density, and insulin-like growth factor-1 (IGF-1) concentration. We tested for differences in metabolic strategy between even and odd year-brood lines of juvenile pink salmon hypothesized by Beamish (2012) using data collected over ten years (2003-2013) from the Bering Sea and Arctic Ocean. Specifically, we predicted that odd juvenile pink salmon would be longer and have greater IGF-1 concentrations, reflecting their tendency to allocate

more energy in the summer towards growth rather than fat storage. Conversely, we predicted that even juvenile pink salmon would have greater weight-length residuals and higher energy density.

3.2 Methods

3.2.1 Field sampling

Surveys were conducted each year from 2003 to 2013 (except 2008) in the Bering Sea. Juvenile salmon were collected using a midwater rope trawl (model 400/300) made by Cantrawl Pacific Limited of Richmond, B.C., Canada. The net is approximately 198 m long and has hexagonal mesh in the wings and body, a 1.2-cm mesh liner in the cod-end, and a mouth opening of approximately 55 m horizontally by 15 m vertically. It was towed at or near the surface for 30 minutes at speeds between 3.5 and 5 knots at each station. More detailed descriptions of surface trawl operations are given in Murphy et al. (2003) and Farley et al. (2009). All sampling was done during daylight hours, from approximately 0700 AKDT to 2300 AKDT. Standard biological measurements, including fork length and body weight, were recorded.

Oceanographic data were collected at each trawl station immediately prior to deploying the trawl. Vertical profiles of temperature, salinity, chlorophyll-a fluorescence, light transmission, and photosynthetic available radiation (PAR) were measured with a Sea-Bird Electronics Inc. SBE 25 Sealogger Conductivity-Temperature-Depth profiler (CTD). Surface temperature and salinity data were measured continuously with a thermosalinograph mounted aboard the ship.

For all years, the NEBS was surveyed between the end of August and during the month of September. However, there were significant variations in sampling extent in 2007 (see Chapter 2, Figure 2.1). In addition, over the course of the survey there was variation in the mean

station latitude, longitude, depth, and Julian day (Figure 3.1; Appendix I), and variation in annual mean environmental variables (Appendix II). During 2013, flooding aboard the vessel resulted in the loss of juvenile pink whole-body and blood samples.

3.2.2 Biological measurements

Length was used to assess size of juvenile pink salmon (Appendices IV, V). Condition was assessed by weight-length residuals and length-specific energy density (calories/g; Appendices IV, V). Insulin-like growth factor-1 (IGF-1) concentration was measured as an indicator of recent growth rate (Appendixes IV, V). The endocrine system regulates physiological processes such as growth. Therefore, growth hormones, such as IGF-1, have been proposed as possible indicators of somatic growth (Beckman 2011). A review of the literature suggests that the relationship between feeding level and IGF-1 concentration is strongest when integrating growth over a 2-4 week period (Beckman 2011).

Up to 50 individuals of each species were sampled haphazardly at each station and measured aboard the vessel for fork length (to the nearest mm) and weight (to the nearest gram). A linear regression of log-transformed weight (g) against log-transformed length (mm) was performed. Regressions were pooled over stations and years. Length-weight residuals were calculated from the fitted models and used as an index of body condition. Two individuals per station were haphazardly sampled for measurements of whole body energy density. Whole bodies of juvenile salmon were stored at -80°C and shipped to Ted Stevens Marine Research Institute (TSMRI) in Juneau, AK, at the end of the cruise. At TSMRI, juvenile chum and pink salmon energy densities were determined using bomb calorimetry, following the method described by Andrews et al. (2009). Prior to bomb calorimetry, fish were weighed (g) and otoliths and stomach contents were removed. Fish were dried in a VWR 1324 convection oven at

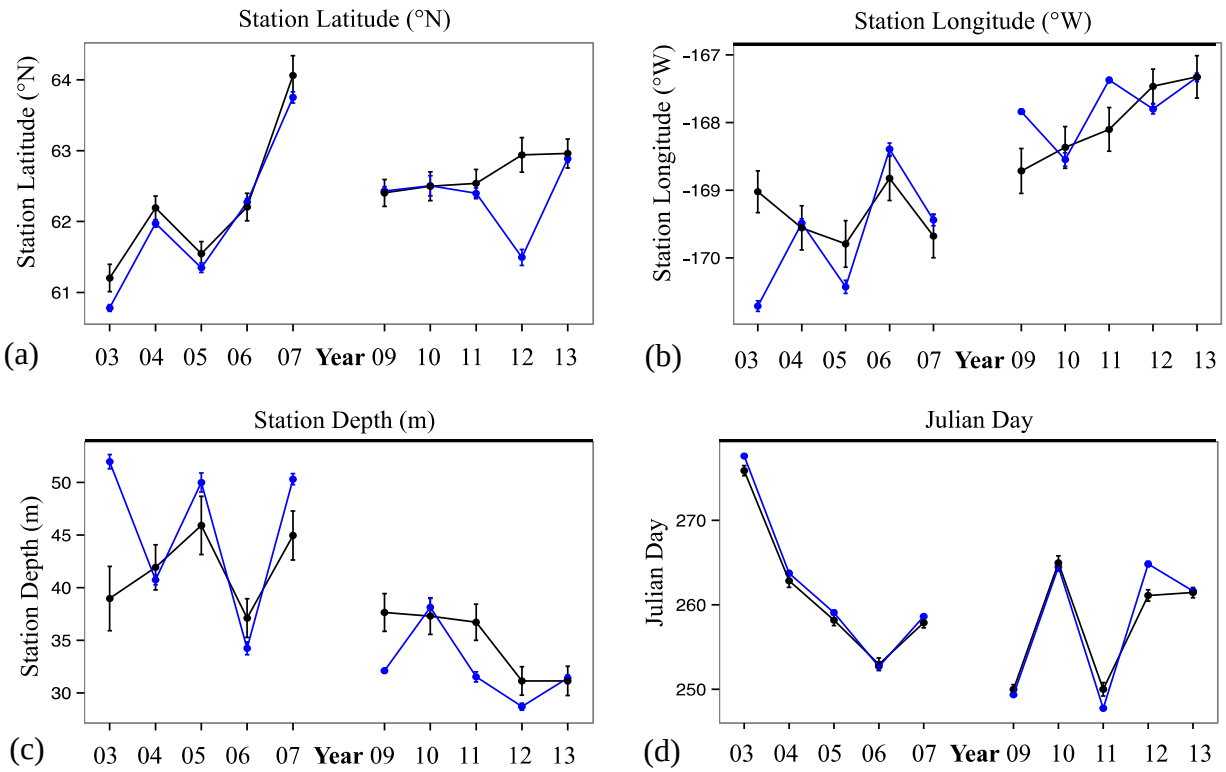


Figure 3.1 Differences in station location and sampling time between 2003-2007 and 2009-2013 from all stations (Black) and stations where pink salmon present (Blue). (a) Mean station latitude, (b) mean station longitude, (c) mean station depth, and (d) mean Julian day of sampling.

60-65° C until a constant weight (within 0.005 g) was obtained. Individual fish were then homogenized using a pulverizer for 30 seconds and then transferred to a mortar and pestle and pulverized further until a uniform powder was obtained. For each sample, pellets were pressed using approximately 0.15 g of powder. Pellets were then combusted in a Parr 1425 Semimcro calorimeter to determine whole-body energy content (WBEC). The values generated by the calorimeter were converted from calories/g dry weight to calories/g wet weight.

IGF-1 concentrations were determined via blood samples from up to 10 individuals of each species from each station. Fish were bled using a heparinized syringe to draw blood from the ventral side of the caudal peduncle. Bleeding of fish < 130mm in length was accomplished by cutting the tail off at an angle at the caudal peduncle and collecting the blood in a microhematocrit tube. Samples were kept on ice (up to 4 hours) until centrifugation. Samples were spun at 3000 x g (~5000 rpm) for 5 minutes and plasma was removed. Centrifuged plasma samples were kept on ice until they were frozen at -80 °C. Plasma samples were sent to the Northwest Fisheries Science Center in Seattle, WA where plasma IGF-1 concentrations were quantified by means of TRF-immunoassay, following the methods of Ferriss et al. (2014).

3.2.3 Statistical analysis

To better distinguish even/odd differences from inter-annual variability in environmental conditions influencing growth and energetic status, we first determined what environmental variables best explained variation in size, growth, and condition of juvenile pink salmon (Chapter 2). Mixed-effects models (Zuur et al. 2009) were used to determine what environmental variables significantly explained inter-annual variation in size, condition, and growth. In energy density models, length was included as a covariate and calories/g and length were log-transformed to achieve normality. Length (log-transformed) was also included as a covariate in

IGF-1 models. For all models, station was included as a random effect to account for possible pseudo-replication.

We added brood-year as a categorical variable to the size, condition, and growth models with the lowest AICs score (from Chapter 2) to determine if there were significant differences in length, weight-length residuals, or energy density between stocks of juvenile pink salmon.

3.3 Results

Length did not differ significantly between even and odd stocks of juvenile pink salmon within the NEBS (Figure 3.2a; Table 3.1). However, odd stocks had significantly greater IGF-1 concentration than even stocks (p-value = 0.003; Figure 3.2d; Table 3.1). Consistent with the hypothesis of greater energy allocation to fat storage in even stocks, we found that even stocks had significantly greater energy density (p-value =0.056) and significantly greater weight-length residuals (p-value = 0.027), compared to the odd stocks (Figure 3.2b,c; Table 3.1).

3.4 Discussion

Our results suggest that even stocks of juvenile pink salmon may allocate more energy towards fat storage than growing in length in the summer, compared to odd stocks. This is evident by the significantly greater weight-length residuals and energy content of the even stock. Furthermore, the significantly higher IGF-1 concentrations of the odd stocks of juvenile pink salmon may reflect a greater allocation of energy towards growth in length, rather than fat storage. These results may reflect differences in metabolic strategy between even and odd stocks of juvenile pink salmon within the NEBS and support the hypothesis set forth by Beamish (2012).

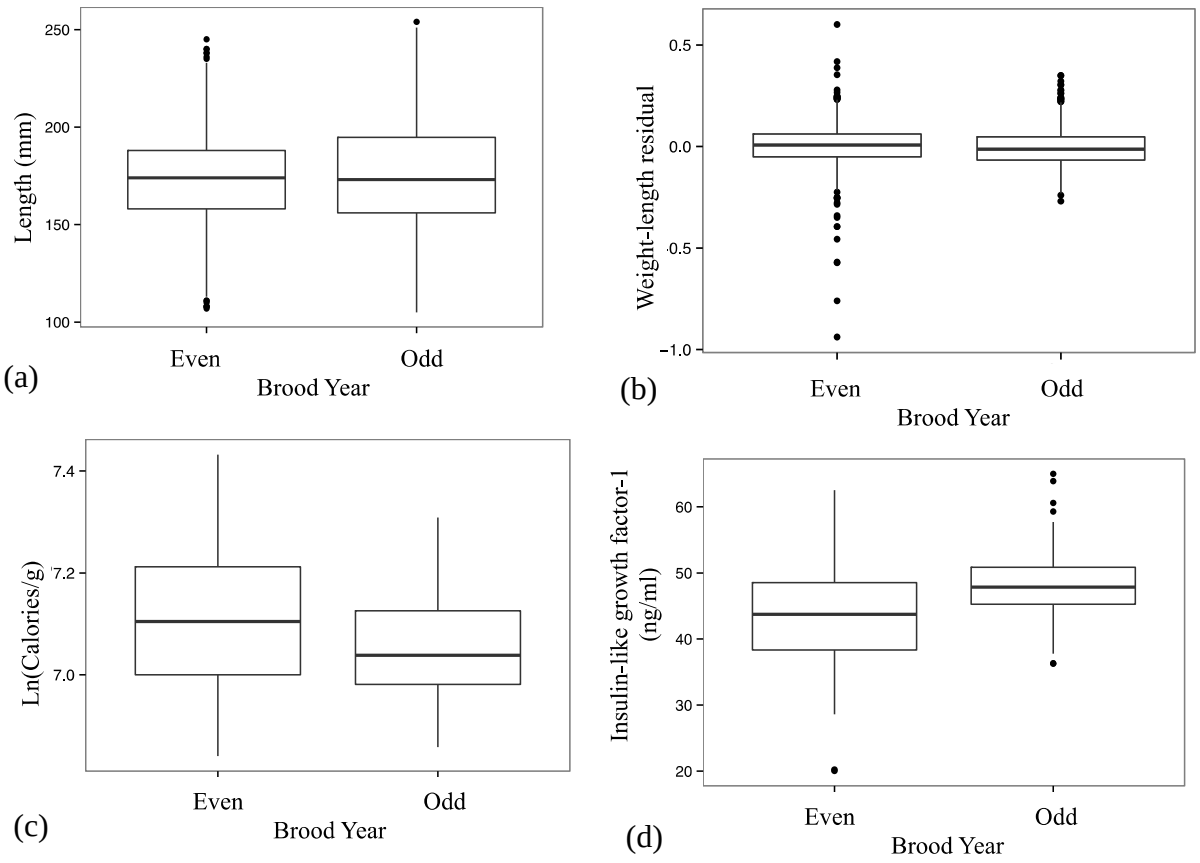


Figure 3.2 Boxplots of juvenile pink salmon showing median, interquartile range, and individuals outside of interquartile range of physiological measures between odd and even brood-year stocks. (a) Length (mm), (b) weight-length residuals, (c) ln (calories/g), and (d) IGF-1 concentration.

Table 3.1 Model coefficients and p-values from models testing for significant differences in juvenile pink salmon responses between even and odd brood-year stocks. Value in parenthesis is standard deviation.

		Fixed Effects		Random Effects	
Model	**Intercept**	**Even Brood-year**	**Brood-year Pvalue**	**σ^2A**	**σ^2B**
Length ~ Brood-year +Julian day + SST + Depth	-158.319 (33.816)	0.142 (2.113)	0.947	14.298	12.664
Weight-lengthresidual~Brood-year +Julian day +Depth	0.180 (0.122)	0.018 (0.008)	0.027	0.051	0.073
ln(Calories/g)~Brood-year + ln(Length) + Depth	4.654 (0.281)	0.029 (0.015)	0.056	0.064	0.062
IGF-1 ~Brood-year + Length + SST + SSS + Depth	2.930 (30.317)	-4.856 (1.484)	0.003	3.028	5.890

Our analyses failed to find differences in length between stocks. However, this result is not enough evidence to conclusively reject differences in energy allocation between stocks. Although we attempted to account for inter-annual variability in growing conditions, it is possible that additional annual variability in length may have obscured differences between even and odd stocks over the limited number of years we were able to analyze (See Ch.2, Figure 2.4a). In addition, while both stocks were similar in average size (Figure 3.2a), length measurements alone do not provide a measure of growth rate. IGF-1 concentration has been shown to be an accurate measure of recent relative growth rate for teleost species (Beckman 2011), and may be more informative than length measurements when testing for differences in energy allocation.

3.5 Conclusion

Differences in energy allocation between even and odd stocks of juvenile pink salmon have implications for how these two genetically distinct lines of salmon may respond to changes in climate. Beamish (2012) attributed the increase of odd pink salmon along the central coast of British Columbia to their ability to take advantage of greater fall and winter zooplankton production resulting from warmer winters. Currently, odd stock abundances are relatively low in western Alaska (Ruggerone et al. 2003; Beacham et al. 2012). However, as sub-Arctic and Arctic climate continues to warm, increased production in the region may support the growth of these stocks.

4.1 General conclusions

We hypothesized that juvenile chum and pink salmon would be longer during warm years and more energy dense during cool years. In years with cool springs, pink salmon were shorter and chum salmon exhibited greater energy density, but no other aspects of size and condition differed significantly between spring thermal regimes. We further examined relationships between size, growth, and condition of juvenile salmon and environmental variables within the NEBS. For both species, length increased with Julian day; longer individuals were caught at stations with greater bottom depths and in cooler sea-surface temperatures, while individuals with high length-corrected energy density were associated with cooler temperatures and shallower station bottom depths. We used insulin-like growth factor-1 (IGF-1) concentrations as an indicator of relative growth rate for fishes sampled 2009-2012 and found fish exhibited higher IGF-1 concentrations in 2010-2012, than in 2009. IGF-1 concentrations were positively correlated with temperature for juvenile chum salmon and with depth and length for juvenile pink salmon. The consistent appearance of depth (indicating distance from shore) in the best size and condition models reflects that longer salmon, with reduced condition, were caught at stations with deeper bottom depths. These results may reflect that fish were allocating more energy to growth than fat storage over the course of the surveys. These results may also reflect the effects of ocean conditions between water currents on salmon physiological response. The cooler, nutrient rich waters of the BSW may provide higher prey availability and feeding success, resulting in enhanced growth of juvenile salmon compared to those caught in the warmer, nutrient limited waters of the ACC. The association between cooler temperatures and greater energy density and longer lengths may reflect indirect and direct effects of temperature on salmon physiology. For example, lab studies have shown that cooler water temperatures result in

an increase in whole body energy content in coho and pink salmon, suggesting that cooler temperatures may signal increased fat storage (Heintz 2009). Additionally, cooler temperatures are indicative of productive BSW, and of wind-mixing and upwelling events that serve to increase productivity within the ACC. Overall, recent conditions of the NEBS correspond to recent increases in condition and growth (IGF-1 concentration) of juvenile salmon, possibly reflecting successful use of higher latitude regions as summer feeding habitat.

This dataset provided the opportunity to compare indicators of energy allocation between even and odd brood-year stocks of pink salmon. We found the even brood-year stocks were more energy dense while odd brood-year stocks exhibited higher growth rates. These results support the hypothesis of Beamish (2012) and reflect differences in energy allocation between brood-year stocks of juvenile pink salmon. As a result, the two brood-year stocks may respond differently to changing climate.

Our results reflect recent patterns in size, growth, and condition of juvenile chum and pink salmon within the NEBS. However, there are many challenges associated with working with a multi-year oceanographic survey dataset. Funding is not consistent and research objectives change over time, resulting in temporal shifts in survey extent and timing. Furthermore, while the BASIS surveys were salmon focused, the main goal of the Arctic Eis surveys was to assess the distribution and abundance of multiple species with an emphasis on species inhabiting the Chukchi Sea.

The BASIS survey expanded into the southern Chukchi Sea in September of 2007 and found significant numbers of juvenile chum and pink salmon (Moss et al. 2009). The logistics of the Arctic Eis survey resulted in the southern Chukchi Sea being surveyed at the beginning of August in 2012 and 2013. The Arctic Eis surveys extended into the northern Chukchi Sea before

surveying the NEBS in September. During the Arctic Eis surveys, few juvenile salmon were sampled in the Chukchi Sea. While we cannot be certain, the lack of salmon sampled in the southern Chukchi is likely a consequence of sampling time. The limited number of juvenile salmon sampled resulted in the exclusion of Chukchi Sea stations from this thesis.

In addition to differences in survey timing and extent between years, the sampling design of oceanographic surveys offers a set of challenges regarding statistical analysis. Juvenile salmon sampled from a single station are not statistically independent from each other (Hurlbert 1984), particularly with regard to associated environmental data. Thus, our samples may suffer from pseudoreplication. To address this issue, we employed linear mixed-effects models. The utility of linear mixed-effect models lies in their ability to account for variation from a set of fixed and random effects (Zuur et al. 2009). Holding sampling station as my random effect allows for random variation within and between stations, accounting for pseudoreplication.

Despite the implementation of modeling techniques to deal with pseudoreplication, analysis of fisheries data remains complex. While we accounted for within and between station variability, model results do not explicitly account for spatial variation within the NEBS region. Instead, linear mixed effects models were used to 1) test for significant differences in juvenile salmon size and condition in the NEBS between warm and cool spring thermal regimes of the SEBS, 2) determine relationships between environmental conditions and juvenile salmon size, growth, and condition within the NEBS, and 3) test for significant differences in juvenile pink salmon size and condition between even and odd brood-year stocks. However, Farley et al. (2005) used generalized additive models to show multiple salmon stocks are sampled within the NEBS. Variation in outmigration timing, genetic differences between stocks, and the relationship between marine entry and ocean environment may contribute to differences in physiological

measures of salmon stocks. While the focus of this thesis was not on distribution patterns, the results of Farley et al. (2005) suggest that our dataset is likely to be confounded by the sampling of multiple stocks within the NEBS. This does not undermine the results of our analyses, which provide a holistic view of how the NEBS contributes to the growth and condition of juvenile chum and pink salmon. It does however complicate inference of cohort growth rates over time and interpretations related to distance and time from point of marine entry.

We employed a linear mixed effects modeling approach for the analysis of this complex dataset. This approach assumes linear relationships between the response and predictor variables. However, the relationship between juvenile salmon and environmental variables, such as SST, may be nonlinear. For example, the multiple stocks that inhabit the NEBS enter the marine environment at different times. As such, environmental variables such as SST and SSS may influence the growth of juvenile salmon differently depending on when and where they entered the marine environment. Future studies should explore the use on nonlinear mixed effect modeling approaches. Furthermore, in addition to accounting for nonlinear relationships between response and predictor variables, the implementation of nonlinear mixed effect modeling may also account for variation due to mixed stocks.

We found that juvenile salmon were significantly longer during the warm thermal regime and significantly more energy dense during the cool regime. However, variability among years within thermal regimes suggests that differences in salmon physiological responses cannot be solely be attributed to spring thermal regime. Our analyses investigating the relationship between size, growth, and condition of juvenile chum and pink salmon and environmental variables may suggest that over the course the survey, juvenile salmon were allocating more energy to growing longer than to fat storage. However, our results may reflect how differences in ocean conditions

between the major currents of the NEBS influence salmon growth and energy storage. Nonetheless, the results support studies finding a negative correlation between energy density and temperatures (Andrews et al. 2009; Heintz 2009). While the negative relationship between length and SST was unexpected, these results may reflect the indirect effects of temperature on ecosystem function. Cooler temperatures are often associated with events that serve to increase nutrient supply to surface waters (Ladd and Stabeno 2012). Furthermore, lipid-rich species of zooplankton are associated with cooler temperatures (Richardson 2008; Hunt et al. 2011; Eisner et al. 2012; Stabeno et al. 2012b). As such, cooler temperatures may be an indication of greater energy availability to higher trophic levels, such as juvenile salmon. Additionally, the negative relationship between SST and length may reflect the tendency for fish to move offshore, into cooler temperatures, as they grow.

This dataset provided the opportunity to test an emerging hypothesis regarding differences in energy allocation between even and odd brood-year stocks of juvenile pink salmon (Beamish 2012). As predicted by Beamish (2012), odd brood-year stocks allocated more energy to length than fat storage, compared to the even brood-year stocks. The greater average IGF-1 concentrations and reduced average energy density of the odd brood-year stocks reflect this (see Chapter 3, Figure 3.2a, b).

In conclusion, this thesis provides a baseline of patterns in juvenile chum and pink salmon size, condition, and growth within the NEBS. These species of salmon have the most northerly range of all Pacific salmon species (Irvine et al. 2009). Their cold water tolerance and minimal use of fresh water habitat have enabled populations to colonize sub-Arctic and Arctic regions (Craig and Haldorson 1986; Irvine et al. 2009). Furthermore, increases of salmon in the Arctic can be expected as the climate continues to warm (Nielsen et al. 2012). However, if there

are increases in juvenile salmon in the Arctic during the summer, it is questionable how many would be able to move south fast enough in order to survive winter. Therefore, in addition to studies monitoring juvenile salmon in the NEBS region, future surveys should expand into the southern Chukchi Sea. In order to ensure sampling of juvenile salmon, surveys in the Chukchi Sea should take place in September or October.

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Appendix I. Annual station parameter values averaged over all stations and over stations where salmon were captured. Value in parentheses is the standard deviation.

	Latitude °N			Longitude °W			Depth (m)			Julian day		
Year	**All Stations**	**Chum Salmon**	**Pink Salmon**	**All Stations**	**Chum Salmon**	**Pink Salmon**	**All Stations**	**Chum Salmon**	**Pink Salmon**	**All Stations**	**Chum Salmon**	**Pink Salmon**
2003	61.20 (1.08)	61.20 (0.90)	61.20 (1.08)	-169.02 (1.72)	-169.05 (1.57)	-170.71 (1.46)	38.97 (17.07)	36.81 (15.38)	51.98 (12.84)	276 (3)	276 (3)	278 (3)
2004	62.19 (1.27)	61.61 (1.49)	62.19 (1.27)	-169.56 (2.47)	-169.22 (1.56)	-169.49 (1.63)	41.93 (16.17)	41.55 (14.13)	40.47 (11.78)	263 (6)	266 (6)	264 (6)
2005	61.55 (1.13)	61.16 (1.08)	61.55 (1.13)	-169.80 (2.30)	-168.62 (1.40)	-170.43 (1.64)	45.91 (18.56)	38.17 (12.45)	49.99 (15.42)	258 (4)	259 (5)	259 (4)
2006	62.20 (1.36)	61.99 (1.29)	62.20 (1.36)	-168.83 (2.28)	-167.35 (1.50)	-168.39 (1.67)	37.10 (12.91)	28.58 (6.92)	34.24 (11.28)	253 (5)	254 (5)	253 (3)
2007	64.06 (1.46)	63.68 (1.88	64.06 (1.46)	-169.68 (1.66)	-169.80 (1.83)	-169.44 (1.89)	44.96 (12.14)	52.96 (11.12)	50.31 (11.48)	258 (3)	258 (3)	259 (3)
2009	62.40 (1.27)	62.75 (1.30)	62.40 (1.27)	-168.72 (2.23)	-167.68 (0.76)	-167.84 (0.69)	37.64 (12.05)	31.92 (4.09)	32.12 (3.58)	250 (4)	250 (3)	249 (3)
2010	62.50 (1.56)	62.37 (1.95)	62.50 (1.56)	-168.37 (2.39)	-167.71 (2.29)	-168.55 (1.37)	37.30 (13.49)	35.54 (13.47)	38.14 (11.63)	265 (6)	263 (7)	265 (7)
2011	62.54 (1.55)	63.23 (1.39)	62.54 (1.55)	-168.10 (2.54)	-166.56 (1.45)	-167.37 (0.76)	36.71 (13.54)	28.27 (9.33)	31.53 (10.31)	250 (6)	251 (5)	248 (5)
2012	62.94 (1.53)	61.70 (1.42)	62.94 (1.53)	-167.47 (1.58)	-167.43 (0.92)	-167.80 (0.73)	31.14 (8.41)	28.16 (4.39)	28.69 (3.40)	261 (4)	264 (4)	265 (3)
2013	62.96 (1.32)	62.28 (1.31)	62.96 (1.32)	-167.33 (2.04)	-167.53 (1.78)	-167.33 (1.65)	31.13 (9.01)	32.15 (8.47)	31.41 (8.10)	261 (4)	263 (4)	262 (4)

Appendix II. Annual station environmental parameter values averaged over all stations and over stations where salmon were captured. Value in parentheses is the standard deviation.

	Sea surface temperature (°C)			Sea surface salinity (psu)			Chlorophyll-a concentration (µg/L)		
Year	**All Stations**	**Chum Salmon**	**Pink Salmon**	**All Stations**	**Chum Salmon**	**Pink Salmon**	**All Stations**	**Chum Salmon**	**Pink Salmon**
2003	8.21(1.14)	8.29(1.12)	7.57(0.62)	30.16(1.65)	30.43(0.80)	30.98(0.77)	1.27(0.66)	1.23(0.51)	0.96(0.75)
2004	9.87(1.36)	10.32(1.17)	10.28 (1.05)	30.70(1.65)	30.96(0.98)	31.103(0.68)	1.69(1.20)	2.42(1.88)	1.79(1.62)
2005	8.42(1.32)	8.64(1.47)	8.10 (0.81)	30.84(1.09)	30.82(0.68)	31.12(0.40)	1.73(0.91)	2.02(0.86)	1.83(0.85)
2006	8.47(1.48)	8.90 (1.33)	8.37(0.97)	30.02(2.65)	29.14(2.75)	29.53(1.93)	0.78(0.58)	0.79(0.40)	0.60(0.31)
2007	8.49(1.73)	8.60(1.29)	8.66 (1.24)	30.89(4.12)	31.47(0.59)	31.46(0.50)	1.88(1.56)	1.79(1.69)	1.51(1.35)
2009	8.12(1.27)	8.47(1.18)	8.42(1.17)	30.16(2.05)	30.30(1.42)	30.65(0.93)	1.09(1.62)	1.21(0.89)	1.24(0.89)
2010	8.00(1.74)	8.15(1.78)	7.40 (1.50)	30.00(2.54)	29.46(3.09)	30.65(1.04)	1.35(1.34)	1.715(1.10)	1.49(0.78)
2011	7.41(1.58)	7.91(1.69)	7.84(1.59)	30.12(2.51)	29.97(1.93)	30.91(0.65)	2.14(1.62)	2.64(1.69)	2.24(1.86)
2012	6.75(1.69)	7.74(0.78)	7.40(0.43)	30.14(2.25)	29.69(3.02)	30.96(0.27)	2.32(3.20)	1.30(0.56)	1.16(0.48)
2013	7.93(2.04)	8.58(0.92)	8.48(1.02)	29.80(2.10)	29.94(1.08)	29.87(1.30)	1.20(1.77)	0.86(0.66)	0.55(0.29)

Appendix III. Number of stations surveyed each year with annual sample sizes of juvenile chum and pink salmon length, weight, calories/g, and IGF-1 concentration.

Year	Stations sampled	Stations with chum salmon	Stations with pink salmon	Sample size of chum salmon length and weight	Sample size of pink salmon length and weight	Sample size of chum salmon calories/g	Sample size of pink salmon calories/g	Sample size of chum salmon IGF-1	Sample size of pink salmon IGF-1
2003	47	32	31	893	550	48	58	---	---
2004	57	43	46	483	622	21	46	---	---
2005	45	27	29	258	287	46	50	---	---
2006	49	29	23	592	351	30	22	---	---
2007	27	16	14	337	482	29	21	---	---
2009	45	17	15	474	339	20	11	90	55
2010	60	38	27	566	192	36	18	157	39
2011	62	24	22	720	472	37	18	103	59
2012	39	16	10	480	101	28	14	123	53
2013	42	27	27	450	682	---	---	---	---

Appendix IV. Mean annual values of juvenile salmon response variables. Value in parentheses is the standard deviation.

Year	Chum salmon weight/length residual	Pink salmon weight/length residual	Chum salmon calories/g	Pink salmon calories/g	Chum salmon IGF-1 (ng/L)	Pink salmon IGF-1 (ng/L)
2003	-0.02(0.07)	-0.04(0.09)	1105.63(138.37)	1196.03(148.50)	---	---
2004	0.04(0.08)	0.01(0.09)	1132.80(128.91)	1194.40(138.56)	---	---
2005	-0.03(0.07)	-0.03(0.09)	1220.57(158.16)	1260.44(192.89)	---	---
2006	-0.02(0.07)	-0.04(0.07)	1067.06(77.42)	1056.89(48.21)	---	---
2007	0.03(0.06)	0.03(0.08)	1359.88(234.29)	1298.97(175.90)	---	---
2009	0.01(0.07)	0.01(0.08)	1327.966(126.80)	1138.36(97.25)	42.8(6.8)	40.3(5.7)
2010	0.01(0.06)	-0.01(0.08)	1305.76(139.14)	1254.36(119.95)	49.6(7.2)	46.7(7.0)
2011	-0.01(0.06)	0.01(0.07)	1270.37(181.40)	1227.91(158.62)	48.3(9.2)	46.0(7.9)
2012	-0.01(0.09)	0.02(0.10)	1143.06(129.97)	1146.36(69.59)	51.1(7.1)	49.2(4.1)
2013	0.03(0.10)	0.03(0.11)	---	---	---	---

Appendix V. Annual mean length and weight of juvenile chum and pink salmon for each response variable. Value in parentheses is the standard deviation.

	Length-weigh residuals				Calories/g				IGF-1 (ng/L)			
Year	**Chum salmon length (mm)**	**Pink salmon length (mm)**	**Chum salmon weight (g)**	**Pink salmon weight (g)**	**Chum salmon length (mm)**	**Pink salmon length (mm)**	**Chum salmon weight (g)**	**Pink salmon weight (g)**	**Chum salmon length (mm)**	**Pink salmon length (mm)**	**Chum salmon weight (g)**	**Pink salmon weight (g)**
2003	188.36	167.00	73.00	45.90	175.52	176.95	60.85	54.91				
	(33.24)	(33.10)	(33.70)	(26.00)	(37.68)	(32.98)	(37.24)	(31.07)	---	---	---	---
2004	205.44	192.64	96.08	70.82	201.81	194.33	87.90	70.63				
	(20.82)	(22.80)	(29.86)	(26.71)	(17.78)	(21.39)	(27.58)	(26.90)	---	---	---	---
2005	199.62	188.56	81.62	63.14	201.72	190.40	83.28	66.40				
	(17.52)	(20.35)	(23.61)	(21.94)	(18.04)	(23.12)	(24.55)	(25.63)	---	---	---	---
2006	155.12	150.81	36.19	29.30	157.63	152.27	38.33	30.68				
	(13.33)	(12.28)	(9.22)	(8.17)	(11.80)	(12.70)	(8.64)	(8.29)	---	---	---	---
2007	198.67	183.65	86.36	62.32	204.69	183.10	94.83	61.14				
	(20.83)	(19.33)	(25.89)	(23.72)	(22.76)	(16.18)	(29.96)	(19.77)	---	---	---	---
2009	175.80	159.68	57.31	37.55	192.90	158.27	76.80	36.82	184.41	165.82	67.19	41.64
	(21.39)	(14.24)	(22.76)	(11.64)	(18.84)	(18.41)	(23.83)	(12.42)	(22.79)	(14.47)	(24.01)	(13.00)
2010	188.33	179.62	70.57	54.49	200.94	190.83	87.36	66.61	188.66	179.41	70.86	54.77
	(18.83)	(16.73)	(24.04)	(18.20)	(18.47)	(14.55)	(25.59)	(15.35)	(18.42)	(10.25)	(21.79)	(13.28)
2011	167.41	147.34	49.14	29.26	176.05	160.44	56.62	38.39	177.64	161.98	58.18	39.78
	(25.24)	(18.69)	(22.26)	(12.69)	(24.29)	(19.97)	(21.87)	(15.87)	(23.71)	(19.88)	(21.94)	(17.51)
2012	166.56	157.33	46.79	35.29	165.93	158.86	46.18	34.00	170.53	157.34	49.29	33.96
	(16.75)	(9.26)	(15.42)	(7.00)	(19.50)	(8.94)	(17.04)	(4.79)	(18.66)	(9.49)	(17.62)	(6.67)
2013	182.90	174.22	65.80	50.60								
	(16.83)	(13.33)	(19.00)	(13.29)	---	---	---	---	---	---	---	---